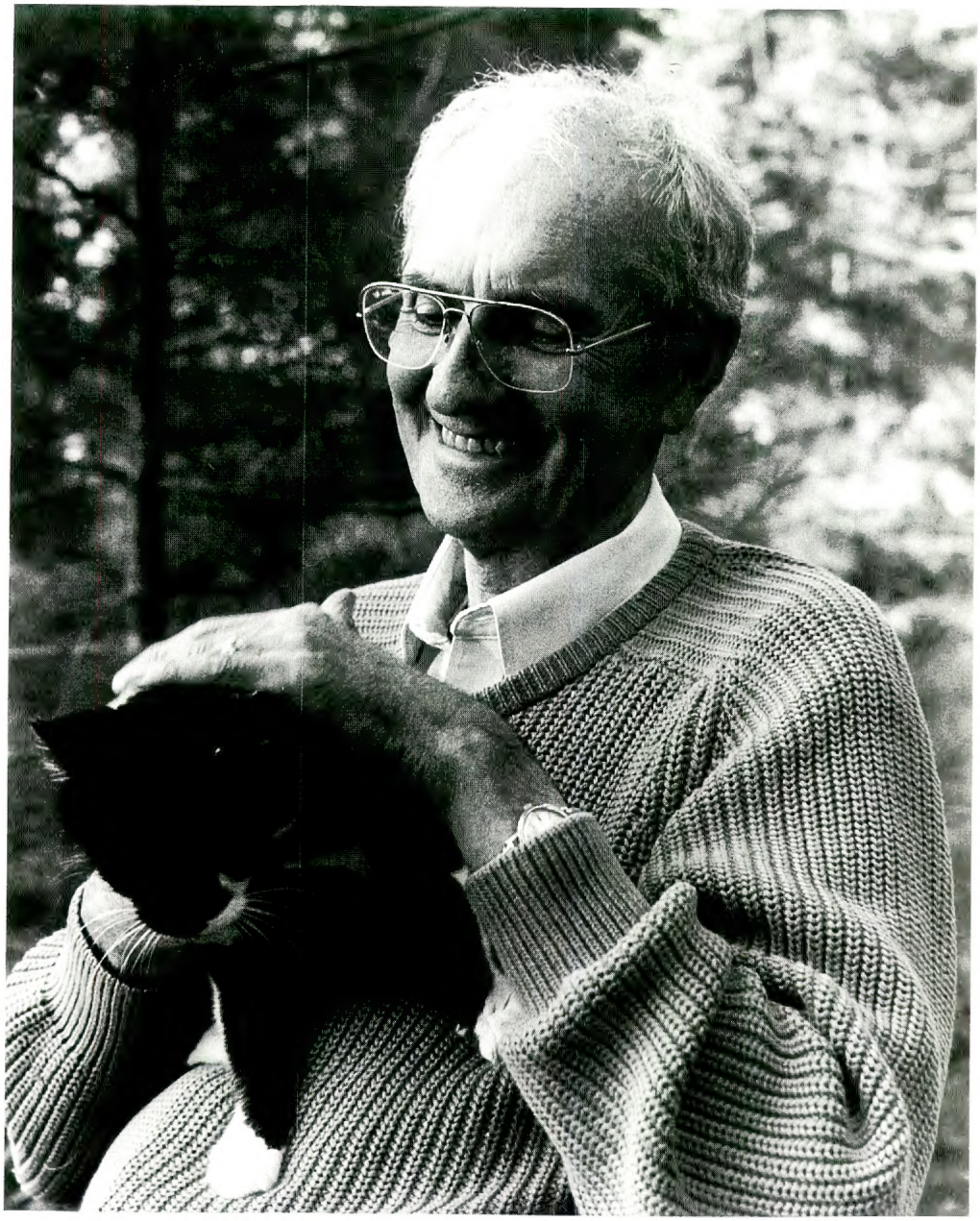
CONTRIBUTIONS FROM THE UNIVERSITY OF MICHIGAN HERBARIUM

VOLUME 18

FESTSCHRIFT IN HONOR OF
HOWARD A. CRUM
IN CELEBRATION OF HIS 70TH BIRTHDAY

University of Michigan Herbarium
Ann Arbor, Michigan
22 August 1992



Howard A. Crum and Hatty

CONTRIBUTIONS FROM THE UNIVERSITY OF MICHIGAN HERBARIUM

VOLUME 18

FESTSCHRIFT IN HONOR OF
HOWARD A. CRUM
IN CELEBRATION OF HIS 70TH BIRTHDAY

University of Michigan Herbarium
Ann Arbor, Michigan
22 August 1992

CONTRIBUTIONS FROM THE UNIVERSITY OF MICHIGAN HERBARIUM

ISSN 0091-1860

Copyright 1992
University of Michigan Herbarium
All rights reserved

Printed in the United States of America

Volume 18

Editor: William R. Buck
New York Botanical Garden

For information about the availability and prices of previous volumes of the *Contributions*, address the Director, University of Michigan Herbarium, North University Building, Ann Arbor, Michigan 48109-1057, U.S.A.

22 August 1992

CONTENTS

Foreword	William R. Buck	1
A tribute to Howard Crum	Lewis E. Anderson	3
Crumuscus vitalis gen. et sp. nov. (Ditrichaceae)	William R. Buck & Jerry A. Snider	39
Key to the moss genera of North America north of Mexico	Dale H. Vitt & William R. Buck	43
A contribution toward a history of the Arctic moss flora	Norton G. Miller	73
Hypnum plicatulum in eastern North America	W. B. Schofield	87
Observations on *Sphagnum fitzgeraldii*	Lewis E. Anderson	91
What is *Lejeunea trigona*?	S. Rob Gradstein	99
Mosses as useful plants	A. J. Sharp	105
Studies on Geocalycaceae VII. Subspecific differentiation of *Chiloscyphus semiteres* together with further refinements in *Chiloscyphus* (s. lat.)	John J. Engel	107
A revision of *Ochrobryum* (Leucobryaceae)	Bruce Allen	113
Reproductive biology of the rare "copper moss" *Mielichhoferia mielichhoferiana*	A. Jonathan Shaw, N. J. Niguidula & T. M. Wilson	131
Beeveria (Hookeriaceae), a new genus from New Zealand	Allan J. Fife	141

FOREWORD

I can't remember when I first met Howard Crum, but after my initial year of graduate study at the University of Michigan I went to the Biological Station at Douglas Lake and there took two of Howard's courses, Bryophytes and Lichens, as well as Ed Voss's Boreal Flora. Although I had had some preliminary contact with bryophytes, I had never sat down and identified them myself. Suddenly I was in class six days a week, and spending evenings and the one "free" day secluded in a dank laboratory keying out moss after moss. Howard had said that his classes always found lichens easier than mosses, and it was true, at least in this pair of classes. It may have been that Howard knew more about mosses and thus taught more, but at least in part lichen species indeed have a more distinctive aspect than moss species. Why, then, would anyone spend their life studying a group of plants with little apparent distinction? The late William Campbell Steere, one of Howard's earliest mentors, was once asked "What good are mosses, anyway?" His response, "They've supported me and my family all these years," has become a classic. However, it is more than the lure of easy money that seduces the unwary into bryology. Whether it be in the field, on hands and knees and peering through a hand-lens, or in the laboratory, gazing through a microscope, mosses have an intrinsic beauty which can be a true Siren to those unafraid to use magnification as an intermediary. I don't know anyone who, from childhood, decided to study mosses. They are too subtle for children, or for most adults for that matter. They are a cultivated taste, but an addictive one. It is to Howard Crum that I owe (or blame) for developing my own fascination with this group of plants.

As a beginning student of mosses, I would work through great piles of unidentified mosses, doing my best to put names on them. Many were from exotic lands (and in those days I had never ventured into the tropics), and identification was further encumbered by guides in German or French. I remember as clear as if it were yesterday, because it happened so many times, that I would struggle for hours with a single specimen until I had exhausted what seemed to be all possible avenues. I would then trundle myself and the vexatious specimen from my basement cell up to Crum's office for assistance. After briefly glancing at the specimen and my prepared slide he would look over, roll his eyes, and say "*Everyone* knows what *that* is!" The obvious implication being, everyone but me! Nevertheless, my attention was held so that next time I would know. I dreamed of the day when I could reciprocate. It only happened once as a graduate student, but it was sweet. In June of 1975 I was going to visit another Michigan graduate student, Joe Beitel, on Long Island, New York. Howard asked me to look for *Sphagnum macrophyllum* and send it to him as living material. The name meant nothing to me at the time, so I went scrambling to the herbarium to see if I couldn't learn to recognize the aspect of the plant. In the pine barrens of Long Island I was delighted to find what I felt surely was *S. macrophyllum*. I put it in a plastic bag and mailed it back to Ann Arbor. Upon returning to Michigan several weeks later I went to Howard's office and there he had the *Sphagnum*, floating in a bowl of water. The first thing he said was "Thanks for the *Sphagnum henryense*." A little disappointed, but not willingly to totally retreat quite yet, I asked if he had examined it with a microscope. He admitted that he hadn't but didn't think he needed to. Nevertheless, I asked that he

just look at it for my sake, and he did. It was *Sphagnum macrophyllum*! Howard mumbled some excuse about not actually knowing the species in the field and never having seen it alive. It was OK. I would never have to endure the "Everybody knows . . . ." again.

From the very beginning Howard Crum and I got along well. We both have a similar sense of humor, and although my expression of it is a bit more tactless and crude, Howard never fails to laugh. (Although usually voting Republican, he is a closet liberal.) We both have what might be called an addiction to gossip. At the Biological Station, Howard had a saying, "If you haven't heard a good rumor by noon, start one!" Whenever I call him, he always wants to be sure he has exracted all the juicy tidbits floating around the bryological community. Early on, Howard became more than just a colleague or mentor, he became a friend. It may seem odd, then, that up until about five years after leaving Ann Arbor, and taking up residence at the New York Botanical Garden, I continued to call him Dr. Crum. There was no implication of formality, it was just the name I used. Finally, in August, 1984, I wrote to ask if I could use his Christian name, since it had become awkward in talking to colleagues about a man I knew better than they did, even if they used his first name. Howard wrote back: "No, since you are no longer so low, I do not mind your calling me by my first name. I understand the awkwardness. I went through it, for example, with in-laws!" Although we continue, as colleagues, to send specimens back and forth for opinions, our friendship has grown. I have shamelessly telephoned him at home to see how his recovery is progressing, from one affliction after another. I got to know his children when they were both young (and Roger a real hellion), so it's still amazing to me that they are grown and married. I have talked with his wife Irene any number of times when Howard was ill, and now I have been conspiring with her about arrangements for the party we have planned for Howard's 70th birthday.

Thus, in late 1990–early 1991, at the meeting of the American Bryological and Lichenological Society at Wakulla Springs, Florida, Dale Vitt and I talked about what we should do to celebrate Howard's 70th birthday. We decided on a combination Festschrift and party at the Biological Station. Unfortunately we were not able, due to space restrictions, to open up these pages to all those who would have liked to contribute. For that I apologize. We decided only to invite manuscripts from former students and close colleagues. Although in the midst of editing the massive *Moss Flora of Mexico* that Howard has been shepherding through publication, I was pleased to take on the editorial tasks engendered by this Festschrift. It provides tangible evidence of my affection, admiration and respect for Howard Crum. On this occasion of Howard's 70th birthday and approaching retirement, I, and the entire bryological community, wish him congratulations and many more happy years of bryology.

William R. Buck

Contr. Univ. Mich. Herb. 18:3–38. 1992.

A TRIBUTE TO HOWARD CRUM

Lewis E. Anderson
Department of Botany
Duke University
Durham, NC 27706, U.S.A.

In his tribute to me in a Festschrift honoring my 70th birthday, Howard Crum (1985) wrote that "it is difficult to write about a friend or to evaluate his career when he is still capable of making rebuttal." This was a prescient statement because, now, ten years later, I have been asked to write a comparable piece for a Festschrift celebrating his 70th birthday. There is not really much to rebut, however; for the most part he was kind and generous to me in his tribute. To my surprise, he used discretion and tact in selecting stories about me and his exaggerations were generally within the established boundaries that we tolerate from each other. I will try to be equally discriminating and cautious in the things I write about him; nevertheless, I will probably touch a few tender spots. I think he will expect that and I wouldn't want to disappoint him.

Because we have known each other for so long and have worked together so closely over the years we each have thick folders of incriminating letters from the other that reveal items and thoughts about colleagues and others that neither of us cares to have disclosed. Most of our letters contain, in addition to the business of the moment, ridicule of each other, continuing arguments, attempts at humor, and a large amount of foolishness. As Howard pointed out in his article about me, they contain material that should not be taken out of context. So, I, too, will refrain from mining those letters for that sort of material.

A short while after the aforementioned tribute to me appeared, I received a letter from a friend of his who stated that he learned more about Howard Crum from the article than he did about Lewis Anderson. He probably got this impression because our lives for the past 44 years have been closely intertwined both socially and professionally. A great deal about me will, of necessity, surface in the present article about him. After all, during these years we have collaborated on 23 papers, 10 fascicles of exsiccati and the two volumes of *Mosses of Eastern North America*. The latter work began in 1959 and continued more or less continuously until it was published in 1981. We have been guests in each others homes countless times; we have watched our respective children mature and drift away; we have spent endless hours together in the field and even more hours working side by side in the herbarium, passing slides back and forth; we have had countless extended telephone conversations; and, as noted above, we have carried on a prolific correspondence over the years. We have exchanged philosophies and concepts and we have learned a great deal from each other. We share the same kind of humorous outlook on life and we have long been able to overlook each other's shortcomings and imperfections. We probably understand each other as well as two friends and colleagues can. Furthermore, we both genuinely enjoy our work and we have had fun in our careers and probably wouldn't do anything much different if we had a chance to relive our lives.

Our first meeting was in 1948 at the University of Michigan, where Howard was

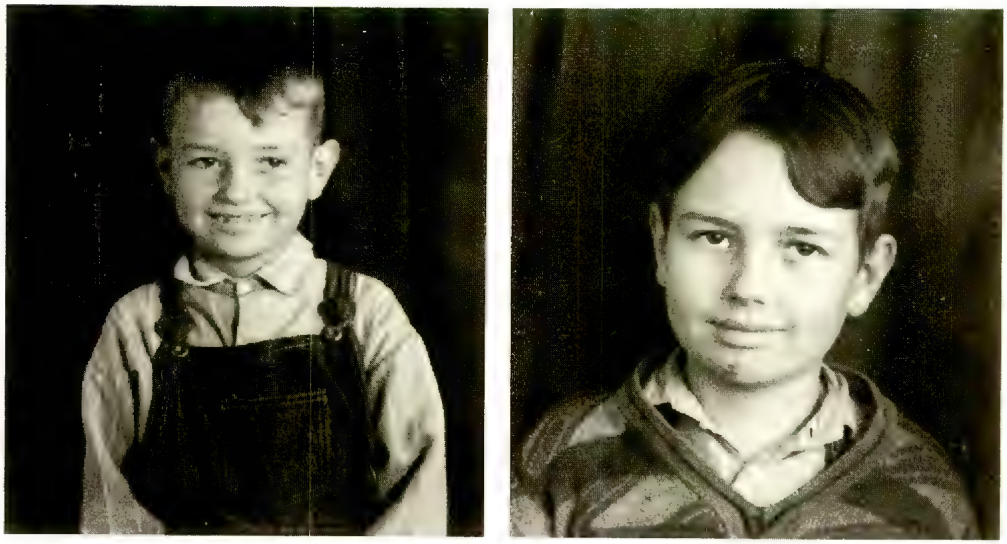


FIG. 1. Howard Crum at age 7 (left) and about ten (right).

a graduate student working with Bill Steere. Howard was among a group of students and myself who were invited by Bill and Dorothy for one of their famous evenings at home. As always at the Steere home, it was a fun evening, with Dorothy plying her guests with food and drink, and Bill cleverly maneuvering the conversation in and out of a delightful mix of light and humorous anecdotes and serious bryology. Students learned without knowing it. Bill had already told me that Howard Crum was by far the best student that had come his way. He cautioned me that Howard was shy and quiet but that underneath there was a deep and penetrating intellect. Steere was right. I hardly knew that Howard was there that night. He scarcely said anything the entire evening; he listened and learned. Later, he told me that he was in awe of Steere and me.

How our close friendship and working relationship has survived these many years is a puzzle to most of our friends and acquaintances. I am not sure that even we understand it. We criticize each other's opinions, ideas, concepts, and even personalities, openly, loudly, and with brutal frankness. We often disagree and our arguments range from playful to vehement. Rarely do either of us win. Those within earshot of our snipes at each other are often astounded, fearful that we are about to end a friendship. We both enjoy telling embarrassing stories about each other. Our colleagues are amazed that our collaboration has endured for so long and that it has been so productive. I think our friendship and collaboration is sustained mainly because we share a mischievous, derisive sort of humor. We work together well because we are comfortable with each other. We say outrageous things about and to each other without malice. I can't recall that we have ever been really mad at each other, although Howard hides his feelings much more than I do.

Howard is easily bored. When we work together, he will often say, "Anderson, you bore me," then tidily put away his tools and depart or demand that we work on something more interesting. Another of his favorite expressions is, "Anderson, I understand you a lot better after I've had a couple of beers." After a time, in a conversation group, he has been known to say, "You people bore me," and promptly leave. Such frankness can be puzzling to some, but however true the

expressions of boredom may be, they are always uttered in jest and reflect partly his puckishness. Mostly, however, his real need is to get away from people. It was a side of Howard that Bill Steere could never understand. When they were working together at Stanford, for example, Howard's need for privacy would on occasion drive him to absent himself without telling Steere or anyone else where he was going or when he was coming back. He would just disappear. Howard might take the bus to Monterey, to the Big Sur, to Muir Woods, to Sonoma Valley or elsewhere and explore the wineries, or to any place that he could be alone.

Wilf Schofield spent the summer of 1957 collecting with Howard in the Canadian Rockies and the Yukon and encountered the boredom trait in Howard. In Wilf's own words: "Peggy [Wilf's wife] joined us in the Yukon for a month. We tented at Mile 1022 on the Alaskan Highway and did most of our collecting there. Peggy would go fishing near a culvert and bring back our meals while Howard and I explored another collecting area. I recall an incident when Howard told us 'You folks bore me; I'm going to go away for a few days.' Since Peggy and I were newly married, I'm sure Howard wanted to give us some time by ourselves, but I suspect that to a degree, we *did* bore him! He returned refreshed, bearing, among other things, fresh *Splachnum luteum*, which I had not seen before".

Students and colleagues who have never met Howard often ask me, "What is Crum like?" Even those who are acquainted with him will sometimes ask me, "What is Crum *really* like?" I only know one Crum: highly intelligent, charming, gracious, courteous, kind, polite, tasteful, cultured, sensitive, and possessed of a tremendously individualized sense of humor. As I have already noted, he is a listener, not a talker. I have never known him to interrupt or break into a conversation and he scarcely ever raises his voice. He is articulate, but soft-spoken with a slight drawl, enough on occasions to be mistaken for a Southerner, which he does not consider flattering. He is not very effective in an oral argument; when pushed into a corner, he simply clams up and grins at you, which takes all the fun out of the dispute.

Howard's listening qualities make him a very effective student advisor. The University of Michigan soon discovered this gift and tapped him for the onerous task of freshman-sophomore counseling. For years he has spent an afternoon or more each week in these counseling sessions. I have learned not to telephone him when he is in an advising session because then he is strictly unavailable to anyone. Those students admire and appreciate him because he is genuinely interested in their lives and problems and he gives them a sympathetic ear. Besides, Howard has an ingrained curiosity. In 1978, he was honored with the prestigious Ruth M. Sinclair Memorial Award for Freshman-Sophomore Counseling, a tribute to his effectiveness.

Along these lines, Jerry Snider reminded me of a story that Irene, Howard's wife, tells about one of Howard's many hospital stays in which he shared a room with an interesting but uneducated man. Howard was very nice to the man, prying with his usual curiosity into every facet of his life. The man was appreciative of Howard's interest and they got to know each other well. The man left the hospital before Howard and, some weeks later, Irene met him on the street. He asked Irene about Howard's health. She replied that he was in the field (meaning with his class on a field trip). The man, looking very downcast, said, "Oh, too bad; oh, how sad," having interpreted Irene's comment to mean that Howard had died and was now in "Potter's Field."

Next to coffee, beer is Howard's favorite drink, although, during his excursions

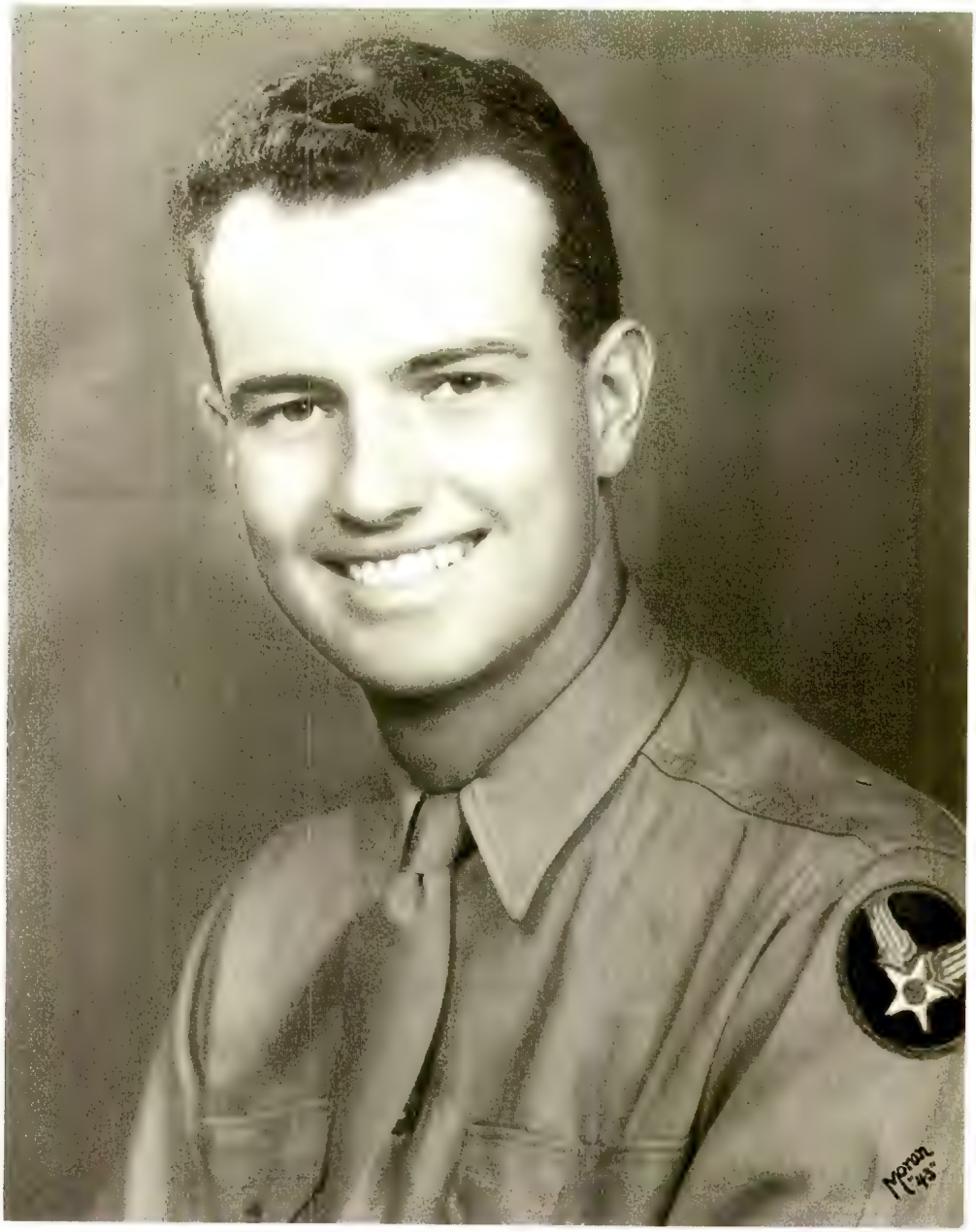


FIG. 2. Howard Crum in uniform during WWII. He served in the Middle East in an intelligence unit in the United States Army Air Force, 1942–1945.

in the southern states, he developed a mild fondness for sour mash bourbon. In the South the tiny, almost microscopic larvae of the chigger or "red bug," are very prevalent in summer. They attach themselves to animal hosts that brush against plants on which the larvae lie in wait. Plant collectors are especially vulnerable as they walk through graminoids and brush, generally at a slow and deliberate pace. The tiny larvae are transferred to shoes and clothing from which they crawl and attach themselves to skin surfaces, causing intense itching and pink or red spots. Humans vary, apparently, in their susceptibility to these pests, and they seem to

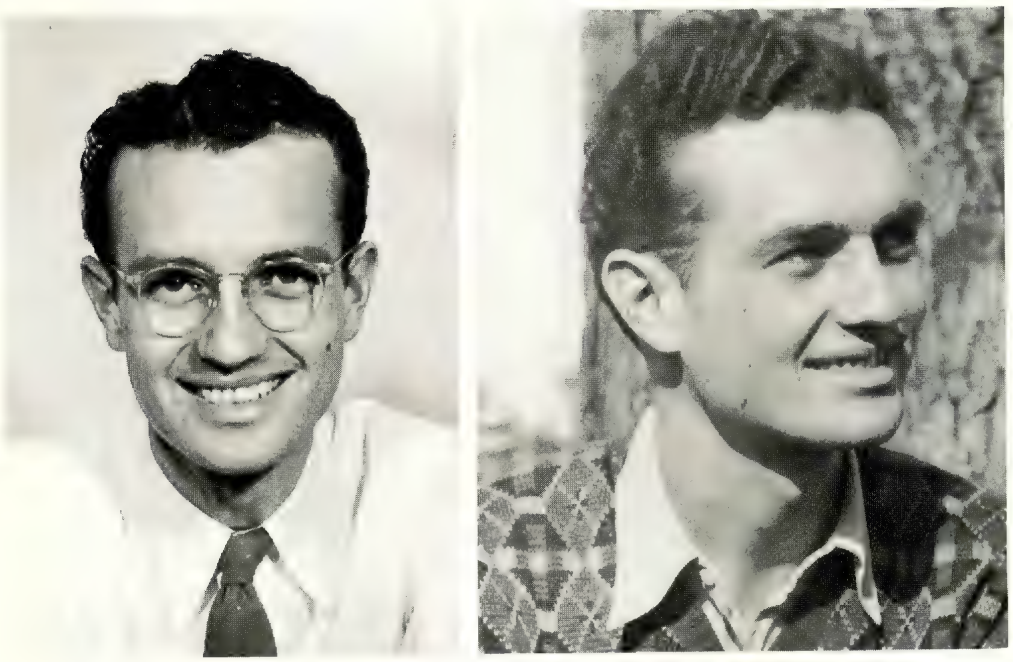


FIG. 3. Howard Crum during undergraduate days at Western Michigan Teachers College (now Western Michigan University).

have a particular affection for Howard. Reasonably effective preventive chemical applications are available but he never seemed to learn how to apply them. On one of our collecting trips to Florida he accumulated a particularly heavy infestation, claiming that he had counted more than 100 of them on his body, some of which he claimed were inhabiting rather embarrassing places. When a motel clerk asked us what we intended to do that evening, Howard replied that he didn't know what Andy was going to do but he intended to retire to his motel room, drink bourbon, and scratch his bites. I quickly explained to the clerk the kind of bites he was speaking about before we were tossed out of the place.

Howard's puckish humor inevitably surfaces at appropriate and often unexpected times and generally cuts right at the heart of the situation. An example is a story that Jack Sharp tells with great relish. Jack, Howard, and the late Bill Fox were collecting in Mexico in 1951. One of their stops was at the Rancho del Cielo, Tamaulipas (Frank Harrison's home), high on the Eastern Escarpment above Antiguo Morelos. They had rented horses and a guide from an Indian village across the river and started toward Rancho del Cielo late in the afternoon (too late for the distance they had to travel, according to Howard's version). It turned out that there were not enough horses for all of them and their luggage and collecting gear. Howard, being the youngest, volunteered to walk. The weather was warm and humid, and the trail was very steep and rocky. As they ascended the high ridge, the trail become rougher and, as darkness approached, one of Howard's legs began to give him trouble. Finally, after several stops because of Howard's leg, Sharp, because he was accustomed to such trails in the Smoky Mountains, suggested that they trade places, which they did. It soon began to rain and as they gained altitude, fog settled in and visibility became zero. Sharp stayed on the trail by holding on to the horse's tail. It continued raining, the fog became even denser, and the guide,

obviously having difficulty keeping on the trail, called a halt to the procession while he did some scouting. After what seemed to be a long period of silence, out of the black dismal night came Howard's voice, loud and angry, "What am I doing here? I hate botany!"

On our field excursions I always drove the vehicle, even if it was Crum's. He will admit under duress, or perhaps several beers, that his driving is somewhat erratic. Those who have ridden with him would call that an understatement. After riding with him in a van at the University of Michigan Biological Station for the duration of his bryology course one summer, the class gave him a Saint Christopher Medal! One summer he wrecked a National Museum of Canada van by crashing into the rear of a car on a straight, level, prairie road. I was never able to wring the particulars out of him. All he would ever say was that he was not picking his nose at the time of the accident. I never would have even learned about the accident but for the fact that he was on his way to Winnipeg, where he planned to leave the van, take the train to Fort Churchill and join Wilf Schofield and me (later, Bill Steere joined us for a while). At the end of our stay in Fort Churchill, he and I rode the train back to Winnipeg to pick up the van and drive to Ottawa. He gave some lame excuse that mechanical trouble had forced him to leave the van east of Winnipeg and that we would have to take a bus to this small town. Of course, there, I learned that in the interim, a garage had made the necessary repairs. In his account of this trip (Crum 1985), these details are omitted.

Howard has had at least two other narrow escapes in automobile accidents (there may have been others that I don't know about), but I hasten to add that he was not driving in either of these. Remarkably, both accidents occurred in Tennessee in different years and both happened when he was returning from collecting trips to Mexico.

In 1949, he joined Bob Wilbur, a fellow graduate student at Michigan, in a joint collecting trip to Mexico. They were accompanied by Bob's brother, who was an engineering student with little direct interest in botany. His and Howard's religious philosophies differed widely, and, according to Bob, they argued almost incessantly throughout the trip. On the return trip, during a particularly high-pitched moment in their argument, with the brother driving, the car ran off the road and crashed into a side ditch. Bob blamed them both equally for the accident.

Returning from Mexico with Jack Sharp and the late Bill Fox in 1951 (the same trip referred to above), nearing Chattanooga, with Fox driving, Sharp sitting beside him and Howard in the rear seat, Fox attempted to pass to the right of a stopped milk truck. The right tires left the pavement and the van flipped over on its side. As soon as he saw that he and Fox were uninjured, Jack looked back and was alarmed that he didn't see Howard. Presently, however, they were relieved to see him emerging from a complete cover of black beans in the corner of the van. Before leaving Mexico, they had bought ten kilos of dried black beans and had placed them on the shelf behind the back seat. The accident ruptured the bag and Howard, unharmed, was buried in the beans.

In 1953, Virginia Bryan, then a graduate student with me at Duke, and I spent most of the spring semester at Stanford University working with Bill Steere on chromosome investigations of California mosses. Bill had obtained one of the very first grants from the newly established National Science Foundation to support the chromosome project. Howard had gone to Stanford after receiving his Ph.D., in 1951, to work with Bill on, among other projects, a flora of Puerto Rico (Crum and Steere 1957), and to help with the identification of Alaskan and other speci-

FIG. 4. Howard Crum as a beginning bryologist, in the field (left, 1946) and at the microscope (right, 1947).

mens that Bill had accumulated over the years. Howard was in his last year there when we arrived. At that time Stanford was a very active place, bryologically. Wilf Schofield, Ed Ketchledge, and Grace Iverson were graduate students working with Bill. Gilbert M. Smith, whom Bill had succeeded, although retired, was still very active. He was revising the bryological chapters of his *Cryptogamic Botany* text and he and Howard had developed a particularly nice and mutually profitable friendship. Douglas Houghton Campbell, who was Smith's predecessor at Stanford, lived on the campus when Virginia and I arrived, but was not active; in fact, he died shortly afterwards. Thus, Campbell, Smith, and Steere, three giants of cryptogamic botany who had occupied successively the same professorial post at Stanford were together at Stanford for a period of time. Having been a member of the faculty there since Stanford opened in 1891, Campbell lived to be 95. In 1959, however, Steere resigned to become Director of the New York Botanical Garden and he was not replaced. The bryological tradition at Stanford, alas, abruptly came to an end.

Howard's three-year stay at Stanford was productive and enjoyable, but it was not without certain frustrations. He had gone to Stanford with high expectations of working closely with Steere and learning from the one-on-one relationship he envisaged. When they were together at Michigan, Steere was chairman of the department and laden with administrative responsibilities. Their contacts there were brief, intermittent, and unpredictable. Among Steere's reasons for leaving Michigan for the post at Stanford was a strong desire to escape the administrative burdens of chairmanship. He claimed that he had no time for research at Michigan, and Stanford promised that they would relieve him of all administrative responsibilities. But, little did they know the strong attraction that administration held for Bill Steere. In a letter to Oswald Tippo, though, Professor H. H. Bartlett, who knew Bill well, summed it up correctly: "[Steere] is a natural-born administrator who can no more keep away from it than he can from his research" (Crum 1977). At Stanford, Steere attracted administrative duties like iron filings to a magnet. It was not long after Howard arrived that Bill, through no fault of Stanford, became as busy, administratively, as he had been at Michigan. (Within a short time he became

FIG. 5. Howard Crum as a graduate student in botany at the University of Michigan, 1949.

Dean of the Graduate School!) As Howard put it, "[Steere] was too busy to help me interpret [species] or to join me in close collaboration" (Crum 1977).

At Stanford, Howard worked in what was called the "back room," which was Steere's laboratory, accessed more or less through Steere's office. The cytological lab, where Virginia Bryan and I worked, was in an adjacent building, but the four of us (and often others) gathered in the back room at mid-morning and mid-afternoon for coffee. These were about the only times that Howard could capture Steere long enough to discuss problems of identification and interpretation encountered in several investigations they were carrying out. One of these occasions produced a Steere expression that Howard and I treasure to this day. Howard had laid aside several sterile specimens that he was unable to identify and hoped that Steere could suggest names. Particularly challenging was a ditrichaceous-looking moss from Panama that had baffled Howard for some time. He reviewed a long list of characters that he had noted, after which Steere turned to him and in all seriousness asked, "But Howard, have you checked the rhizoids?" Of course, Howard had not checked the rhizoids, and there the matter rested! [The moss turned out to be *Garckea phascoides* (Hook.) C. Müll.] Since then, when either of us sends the other a specimen for verification or hopeful identification, the reply is often, "I don't believe you checked the rhizoids!" Thereafter, when Bill would overhear us use this expression, he would always appear puzzled, then give us his characteristic quizzical look, followed by "Oh, really?" Although Bill Steere had a vigorous sense of humor and could and did spiel off one joke after another, they were never jokes on himself. His shortcomings, blunders, and human frailties were not amusing to himself.

The Stanford experience was exhilarating and profitable for all of us. Moreover, it was fun. Howard, Virginia, the late Dick Holm and I spent many delightful evenings sampling the cuisine and splendid wines in the many fine resturants in the

area. In a small group such as this, Howard is at his best, and it was at these gatherings that I got to know him well. I discovered that, unlike Bill Steere, he could laugh at himself and that, indiscriminately, he could combine fun and serious work. Moreover, we liked each other's company. Howard put it best: "Our friendship has been based on mutual interests, scientific and cultural, as well as mutual tolerance for personal foibles, his and mine. We have a similar way of viewing the world and each other, with puckish good humor" (Crum 1985). Thus, when the opportunity came to collaborate, scientifically, we felt that we could work together pleasantly and profitably by combining somewhat diverse talents and knowledge.

Howard spent the summer of 1953 in Alaska with Bill Steere, based at the Arctic Research Laboratory at Point Barrow. They collected together at Barrow and Cape Lisburne and Howard collected extensively at Meade River and the Anaktuvik Pass in the Brooks Range (Crum 1977). Actually, Bill did little collecting that summer. Using the techniques we had worked out at Stanford, he counted chromosomes from material brought in from the field by Howard. This was Howard's first field experience in the High Arctic and the time he had spent identifying Steere's Alaskan material at Stanford provided him with a background knowledge of the moss flora there that greatly enhanced his collecting effectiveness. He also learned to recognize capsules in the proper meiotic stages for chromosome study. Over the years he has sent me much living material for cytological study and, together, we published a long paper on the chromosomes of a large number of mosses of the Canadian Rocky Mountains, based entirely on collections of his that were shipped to me at Duke.

Howard's post-doctoral with Steere ended in 1953 and, after much job-hunting, he accepted a position in the Department of Biology of the University of Louisville. He stayed only one year, however. A position opened at the National Museum of Canada when I. Mackenzie Lamb accepted the directorship of the Farlow Library and Herbarium at Harvard University. Howard applied for the position vacated by Lamb and was appointed Curator of Cryptogams, beginning in the fall of 1954.

In the meantime, I was able to obtain meager funds to support Howard at Duke for the summer of 1954. He helped with the determinations of mosses that I had collected on a previous summer's excursion to the Ozark Mountains. He was grateful for the financial support, but when his first check arrived he was stunned to discover that he was being paid out of a petty cash fund. To this day he reminds me of this humbling experience. Rudy Schuster was in residence at Duke then and it was a memorable summer. Rudy occupied two small rooms adjoining the then small herbarium. Olga, Rudy's wife, did much of his typing directly across the hall from his work room. I know of no couple more devoted and respectful of each other than Olga and Rudy. Their loud, reciprocal arguments, replete with mutual denunciations, strong profanity and vilifications when working together, however, are notorious. The exchanges are totally harmless, but this was Howard's first experience with the Schusters and, on occasion, he would get so nervous he would have to leave and take a walk.

Generally, we used Grout's flora in our determinations and its deficiencies became even more apparent as we worked through the Ozarkian specimens. We soon came to the conclusion that it needed to be revised. The long discussions and experiences we had that summer led eventually to *Mosses of Eastern North America*. First, we decided simply to revise and tidy up Grout's work, a project that we estimated would take no more than three years. Very quickly, we abandoned the idea of a revision of the Grout treatment and decided on an original flora scaled

FIG. 6. A rainy day on Mont Tremblant, Quebec, during the Pre-congress foray, IX International Botanical Congress, August, 1959. Howard organized and led the foray. Harry Williams, Howard Crum, Seville Flowers, Fred Hermann (left to right).

down to include only eastern North America. We realized that such a flora would take more time, but even so, we couldn't have realized that we were beginning a 27-year project.

During that eventful summer of 1954, I discovered many of the talents and skills that contribute to Howard's scientific and scholarly proficiency. I found that he has a broad liberal background in arts and sciences, especially in classics and languages, which is quite unusual for someone trained in the sciences. His tremendous command of the English language is reflected in all his writings. A natural editor, he cannot refrain from tinkering with careless and slovenly writing. He attacks manuscripts with a sort of vengeful glee. When he spots an ungrammatical lapse his lips curl into a determined but pleasing grin. Thus, when Bill Steere called me in July to report his appointment as Dean of the Graduate School at Stanford and to tell me that he could not possibly edit *The Bryologist* any longer, he and I agreed that Howard would make a good editor. When I broached this to Howard, he was dumbfounded. Out of graduate school only three years, he was stunned at the prospect of editing a professional journal at this early stage in his career. I reminded him that all the while he was at Stanford he had more than assisted Steere in editing *The Bryologist;* he had handled a lot of it on his own. At the time, I was acting as Business Manager of the American Bryological Society and the journal was being published in Durham. With some prodding from Steere and after taking Howard to the publishing firm, where he met the printing staff and publisher and saw the production operation, he was persuaded to take the job. It was not difficult

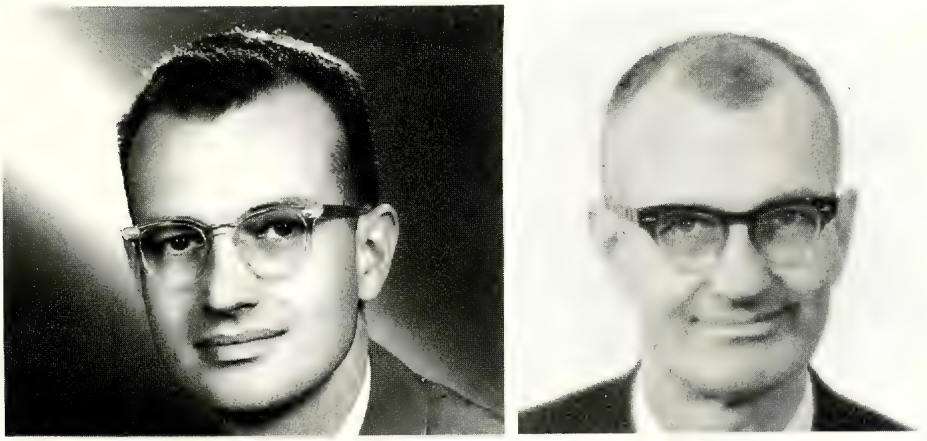


FIG. 7. The hair gets thinner. Howard Crum in 1952 (left) and 1970 (right).

to convince the executive committee of the Society to name him the new editor. He began immediately, editing Number 3 of Volume 57 (September, 1954), while he was in Durham that summer. He was able to work directly with individual members of the publishing firm and gained valuable experience that would help him in future editing. By chance, I was the author of the first paper in that number and I do not need to add that he tackled all its deficiencies with delight.

As Bill Steere and I expected, Howard became an excellent editor. He edited with a firmer pencil than Steere and may have ruffled the feathers of a few authors with his grammatical and stylistic tinkering, but the quality of papers improved during his editorship and *The Bryologist* became a better journal. Among other changes, Howard shifted the journal to a quarterly in 1962. Founded by Abel Joel Grout in 1898, it had begun as a department in the *Fern Bulletin*, which was a quarterly. In 1900, however, *The Bryologist* became an independent journal and, in 1902, it went to six numbers per year, where it remained until Howard's change. In the December, 1955, issue he introduced a valuable "News and Notes" section. Its chatty and informal style has continued through a number of editors to the present. He kept the editorship for two terms or a total of eight years and was succeeded by William Louis Culberson in 1962.

During the summer of 1954, Howard became a fixture in the Anderson household. He was 32 and unmarried. Although he lived in a dormitory room on the Duke campus he spent much time in our home. There were five children, three girls and two boys, seven to twelve years old, including a pair of twins. It was a busy, noisy place, and Howard was fascinated, especially with the girls, seven, eight and eleven. One evening when he was having dinner with us a girlfriend of our oldest boy, Philip, was also a guest. She and Philip were 12. There was a bouquet of snapdragons on the table. Our little guest was sitting next to Howard and at some point asked Howard a question about the snapdragon flower. Always the ready educator, he began explaining the structure of the snapdragon flower to her at a technical level that was beyond anything the poor girl could comprehend. Also, it soon became clear that she knew very little about the sexual life of the flower or for that matter, animals or humans. As her questions became more pointed and precise, Howard found himself in the awkward position of having to explain sex to this innocent child. He made a number of clumsy and embarrassing starts, but he was totally unprepared for the challenge that soon unfolded. He looked to all of us in

despair, expecting help that never came. He never forgave us for the silence and for giving him no help whatsoever. Finally, my wife, Pat, came to the rescue by telling the girl that the flower produced seed, which, when planted, produced another plant. That satisfied the youngster and Howard was finally off the hook.

After he was married and had children of his own such conversations with them would become more natural. Howard told me rather recently of an incident that occurred when his children, Roger and Mary, were in their pre-teens. Roger's elementary school teacher (and presumably others) had given a sex education lecture to his class and some of the parents were apprehensive about its content. The parents were invited to come to the school one evening and listen to the lecture as it was given to the students. Roger's parents attended. When they returned, Roger asked his father how he liked the lecture. Howard replied, "Well, it was very instructive and educational, but they didn't tell you how much fun it is!" This episode illustrates the kind of open and frank relationship he always kept with his children, even when they were very young. He always treated them as adults.

In early September, 1954, we went to the Gainesville, Florida, AIBS meeting with Heinie Oosting and Terry Johnson. [Howard, in his account of this trip (1985), incorrectly included Bill Culberson in the group.] Terry and Howard were graduate students together at the University of Michigan and knew each other quite well. Howard, in his account, refers to ". . . night disturbances resulting from sophomoric humor," without further elaboration except that "The situation would not have arisen except for Heinie's cautious use of the dollar, which resulted in our sleeping five [actually four] to a room." Terry and Howard shared one bed and Heinie and I the other. Howard is a light sleeper. After retiring, he would stay awake for a long time, get out of bed often, and walk around in the room until he felt sleepy. Terry went to bed early, slept soundly, and arose at an unearthly hour, such as four A.M., wide awake and ready to go! As Heinie complained, by the time Howard quit getting up and bumping around in the room, Terry was up, shaving and showering. On one particularly bad night, Howard, still wide awake at midnight or one A.M., gave the sleeping Terry several stiff jabs with his elbows. Terry sat upright, inquiring, "What's wrong, Howard?" Howard said, "Terry, I've just wet the bed." Terry jumped out of the bed, knocking over a table and lamp and waking Oosting and me. Of course, Howard had not wet the bed, but there was little sleep for any of us thereafter. Sophomoric humor?

Almost immediately after arriving at the National Museum Howard made plans for Canadian field work, which the Museum encouraged. He spent succeeding summers collecting in the Gaspé and Laurentian Mountains, the Bruce Peninsula and Niagara Escarpment, the Canadian Rocky Mountains, the Yukon, and northern Manitoba.

In 1957, he and I made a firm commitment to work on the moss flora of eastern North America. We applied for and received a grant from the National Science Foundation and very shortly signed a contract with Columbia University Press to publish the work. I spent most of the winter and spring of 1959 in Ottawa. We worked together, side by side, each with microscopes, passing slides back and forth and trading jibes and information. This was the real beginning of the flora.

Howard had just bought and moved into a new house when I arrived and I occupied one of the bedrooms during my stay, which extended into the spring. It was during this stay that Howard claims I gave him stomach ulcers, which ultimately necessitated rather drastic surgery. This was followed by a siege with his gall bladder, which I maintained was brought on by his greasy cooking. Actually he was a

good cook and produced some real culinary treats. But, unfortunately, he was fond of fatty foods, including something the English call fried bread, which consists of soaking and frying slices of bread in left-over bacon grease. I found the result utterly loathsome, and rejected it on sight.

The brightest parts of our working days at the National Museum came when Irene McCarthy stopped in and visited with us. She was Administrative Secretary in the Department of Botany and we looked forward to her visits. Attractive, vivacious, cheerful, spirited, extraordinarily intelligent (much smarter in a non-academic way than Howard), incredibly organized, the neatest and tidiest person I have ever known, she managed the affairs of that department with stern, unyielding efficiency, and with a tremendous sense of humor. She was not intimidated in the slightest by a scientific staff of all-male prima donnas, including the chairman, A. E. Porsild, a noted authority on arctic plants. She radiated brightness and cheerfulness in the otherwise gloomy atmosphere of the then old and stuffy museum building with its high, multistoried lobby overcrowded with tall, dusty totem poles.

I soon noticed that she and Howard were quite friendly. They enjoyed sharing gossip; they joked and kidded each other; they had formed an alliance against staff members they disliked; they obviously liked each other. He called her McCarthy then, never Irene. Of course, I joined the good-natured bantering, which provided intermittent relief from the daily tedium of looking at herbarium specimens, supervising a recalcitrant but gifted artist, and constant decision-making.

At first I thought something might be developing between them, but soon dismissed it because I knew they were not seeing each other except in the herbarium. That was certainly no place to carry on a romance. Howard did ask me once if I thought McCarthy would make a good wife. My answer was a stream of praise for her and an enumeration of all the splendid qualities that I had observed during our brief acquaintance. I reminded him, however, that she was too smart to marry him, a deep-rooted, fastidious bachelor, whose habits and mores were indelibly fixed. As it turned out I was quite wrong.

They were married on December 26, 1960, after what has to be one of the strangest courtships on record. She recently filled me in on the particulars, and they are worth recording. At the time, the fall of 1960, the Canadian government was in the midst of a campaign to encourage its employees to become bilingual and were providing free language courses for them. On this particular day Irene and Howard were discussing the possibilities of enrolling. Irene had already decided that she didn't want to register for a French course, which was the principal language being pushed. Rather, she told him, she wanted to be different and intended to register for a biology course, which might help her in her work. Howard replied, without any hesitation or change in inflection, "Well, if you want to be different, then why don't you marry me?" At first she thought he was joking, but he was serious. Moreover, he wanted to get married that weekend! She would have none of that, so they were married the day after Christmas, with all of the appropriate rituals of a traditional wedding.

Irene tells me that when Howard first joined the museum staff she thought he was pretty cute. Presently, she began to make a conscious effort to attract his attentions toward her. As time went on, however, she saw no results of this encouragement and after a couple of years decided that it was a hopeless cause. Although they established a pleasant relationship at the Museum, it never went beyond that. He never dated her once; he didn't take her anywhere, not even to a movie; they never had lunch or dinner together; they never even took a walk together. It is,

FIG. 8. Irene and Howard Crum, married and intent on starting a family.

therefore, no wonder that she had given up. When the off-handed proposal finally came she was stunned and she could scarcely wait to tell her mother. After dashing into the house and loudly exclaiming that she was getting married, her mother, having forgotten about Howard, replied, "To whom, for goodness sake?"

I was right about one thing, though. Irene turned out to be the kind of wife that I envisioned and much more. She is the only woman that I can think of that could have sustained a happy marriage with Howard. They have a fantastic marriage and a mutually satisfying home life. Pat and I have been guests on numerous occasions over the years and have watched their children mature. Irene is a wonderful cook. Her specialties are desserts, and she and I share a love for them. We also share a struggle with our respective weight levels. Irene is an impeccable housekeeper. She is even more fastidious than Howard. Her house is as clean as an operating room in a hospital. She has looked after him, I am sure, as well as his mother did. He has survived an unbelievable number of life-threatening illnesses principally because of her agressive vigilance.

The two Crum children, Roger and Mary, are highly talented. I don't know of any parents who have enjoyed and relished their children more than Howard and Irene. The children have responded in kind. Roger, now married to Robin, received his Ph.D. in art history from the University of Pittsburgh in 1991, and is now Assistant Professor at the University of Dayton. Mary, a music major with a degree

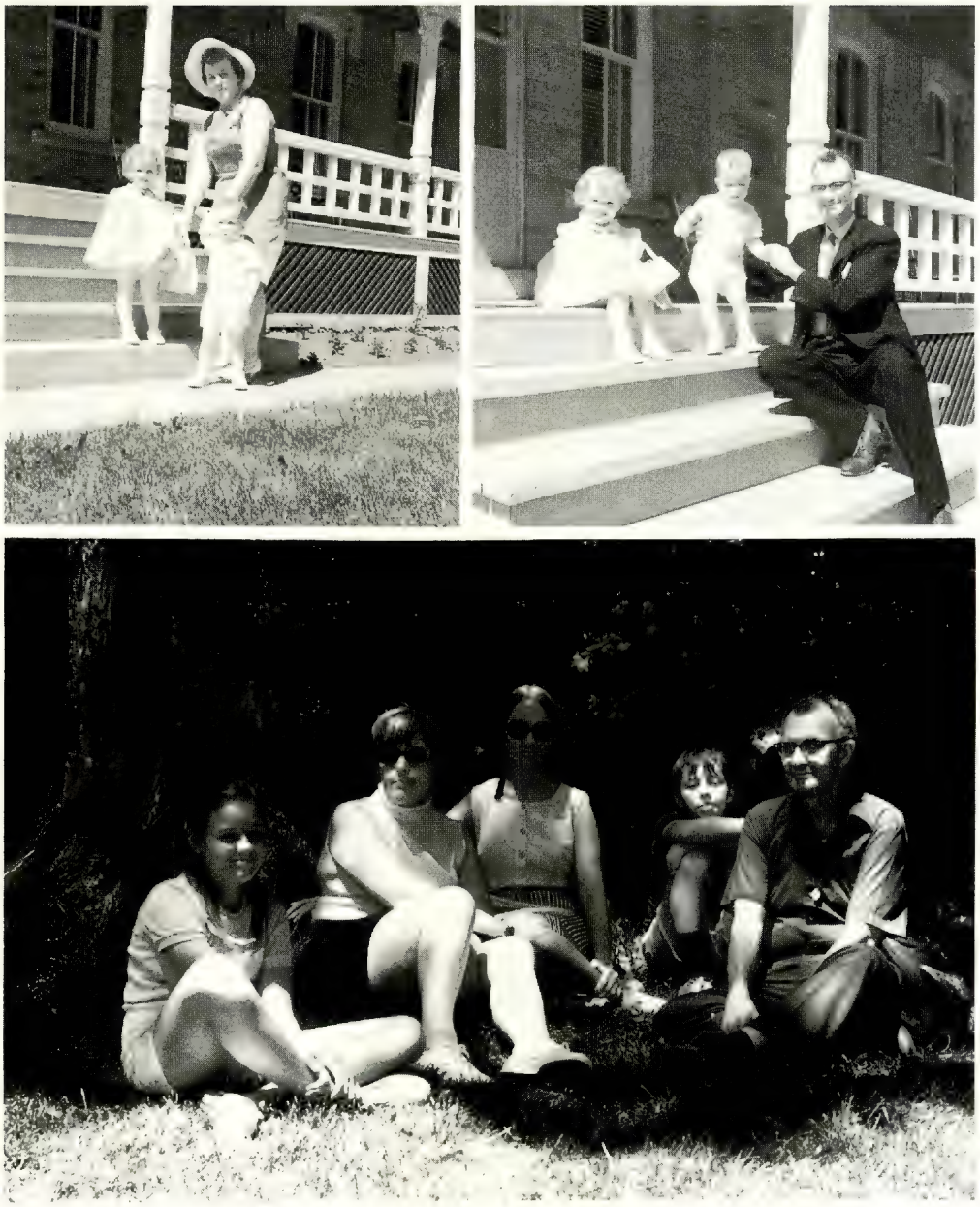


FIG. 9. Irene and Howard Crum learning to deal with toddlers Mary and Roger (above); and on Mackinac Island, summer, 1974, Mary, Irene, Linda (Mrs. Jerry) Snider, Roger, Howard (left to right).

from the University of Michigan, teaches music in the public schools (she is an accomplished clarinetist, and plays beautifully) and is married to Brian Scholtens, who, in 1991, received his Ph.D. in zoology from the University of Michigan, where he now holds a teaching position.

A quote from a recent letter from Roger provides a much better insight into family life than I could possibly write.

"One thing that I've always enjoyed telling people is that, while my father is a botanist, there have never been any plants in our home. You can well imagine why this is so, given that my mother is definitely in charge. Since she grew up on a farm,

FIG. 10. A beautiful bride; Howard, Mary Crum Scholtens, Irene.

dirt of any nature in the house represents something with which to wage constant battle.

"There was never any bryological shop talk at our home, even though hours upon hours of bryological research and writing occurred on my father's lap in the living room. My father could work while any sort of noise, playing or watching of television, was going on. He could work through it all without being disturbed in the least. It seems to me that my father has always worked best at home, in his living room chair (and at times with the two of us in the chair with him), with a manuscript set on a kitchen cutting board on his lap. In fact, as you well know, since Dad has been seriously ill so many times, a good deal of his work has by necessity been carried out at home.

"Finally, bryology has been Dad's thing and Dad's thing alone. He has never spoken of his academic stature or success, and it was years before I understood the importance of his contributions to the field. He showed by his example the joys of an academic life style but he never urged Mary or me to become interested in science or botany in particular. His major interest was that we pursue that which interested us most. As things have turned out, this has been music for Mary and art history for me."

Howard Alvin Crum was born on July 14, 1922, at Mishawaka, Indiana. His mother, Eunice Eva Crum, died in 1949, at age 51; his father, Earl Earnest Crum, called Jack by his friends, died in 1964, at age 73. The father worked as a riveter for the Studebaker automobile factory in South Bend, Indiana, during the 1920's and into the early years of the Great Depression. They had four children, Chester, Roger, Howard and Roland. Howard grew up in Mishawaka, except for one year in which his father moved the family to Howard's grandfather's farm in Burr Oak, Indiana. That one year on the farm made a deep impression on Howard. For years,

FIG. 11. Roger Crum's wedding. Above, Howard, Irene, Roger, Mary. Below, Howard, Irene Roger, Robin, Mary and Brian Scholtens.

FIG. 12. Irene and Howard Crum after Roger's wedding (left) and a happy Howard (right).

I thought he grew up on a farm, because he spoke so much about farm life. After that year the family moved back to Mishawaka.

Howard had a special affection for his mother and speaks of her often. He can get misty-eyed while discussing her. I remember an incident when Pat and I were visiting the Crums in Ann Arbor. I went to the kitchen to mix my five o'clock drink only to find that the ice cubes had frozen into a solid bar of ice. Reaching into the nearest drawer, I pulled out an old, nondescript wooden spoon and proceeded to whack away at the ice to try to break it apart. The spoon shattered into splinters just as Howard walked in. Instead of playing the perfect host and reassuring me that it was nothing, just an old wooden spoon, he gave me a despairing look, and in the saddest voice, said, "It belonged to my mother; you clod, you've destroyed it." There was sadness, of course, over the loss of the sentimental spoon, but mostly he wanted to embarrass me. I reminded him of the time that he was admiring a particularly beautiful and expensive mahogany salad bowl at a dean's house when it inexplicably fractured in his hands.

After attending Kennedy School for grades one through eight, Howard went to Mishawaka High School, graduating in 1939. His two older brothers, Chester and Roger, as well as an aunt, had all attended Western Michigan Teachers College (now Western Michigan University) at Kalamazoo, so Howard followed them there, entering in the fall of 1939. He became a German major, but his university education was interrupted by World War II. He is very proud of the fact that he did not wait to be drafted. He volunteered for the United States Army Air Force in 1942, and served in the Intelligence Division, where he became an expert cryptographer, with duty in North Africa and the Middle East.

As his son Roger has reminded me, Howard, in a very quiet, apolitical way, is a very patriotic person. I have seen him become maudlin upon viewing the American

flag. The flag means more to him than it does to most Americans. He can get genuinely sentimental about the origins and preservation of the ideals of his country. This may surprise people who do not know him well.

Howard returned from military service in late 1945, and spent some time with his mother, who was in ill health in Mishawaka. Like many returning veterans, he began to have some uncertainties about his academic directions. In the spring of 1946, he visited the University of Chicago and interviewed for medical school there. Based on his superb record to that point, they accepted him. He never had any real interest in medicine, however, and eventually decided against it. This was a lucky break for bryology.

Finally, he decided to resume his studies at Western Michigan University, but enrolled at the University of Michigan Biological Station, at Douglas Lake, for the summer session as a student disjunct from Western. He registered for Anatomy, taught by C. D. LaRue, and Systematic Botany, taught by none other than Bill Steere. He claims that "the excitement of being there, in a research environment with the best of students and the best of teachers, predestined me to a career in botany" (Crum 1977). When he returned to Western Michigan it is not surprising that he changed his major from German to botany. Somewhat defensively, he brags that he had always had a real love for plants. He speaks proudly of the fact that both his parents knew the common names for most of the plants in their neighborhood and that his mother was a good gardener.

Contrary to what one might think, Bill Steere did not introduce Howard to bryophytes when he took his systematics course in the summer of 1946. He discovered them the following winter when he returned to Western Michigan. Bill Buck, who knows everything about everybody, told me that Howard's interest in mosses developed as follows. Howard and another botany major, a girl, by the way, that fall began a routine of walking in the woods in order to strengthen their knowledge of plants. With the onset of winter, the tree leaves and flowers disappeared. The only green remaining were mosses and liverworts. They began collecting them and made attempts to identify them, probably with the aid of *Mosses with a Handlens*. They may have had some help from Professor Leslie A. Kenoyer, who was the principal botanist there, but it would have been minimal. There is no indication that he knew much about bryophytes. At some point Howard did accompany Kenoyer on a short trip to Mexico. The professor was a generalist with very broad interests, including systematics, floristics, ecology, morphology, anatomy, and pollination biology. He undoubtedly provided some encouragement for Howard's leanings toward botany, but his interest in mosses was evidently self-induced. Howard became an instructor his senior year at Western Michigan and received the B.S. degree, magna cum laude, in 1947.

Meanwhile, he was awarded a prestigious Rackam State College Scholarship at the University of Michigan, to begin in the fall of 1947. Curiously, in his application for the scholarship he indicated that he wished to major in plant pathology. After graduation, however, Howard decided to spend the summer at the Biological Station, where he enrolled in Margaret Fulford's course in bryophytes. This was the first time she offered it at the Station. Concurrently with her bryology course, he took Professor Gerald Prescott's course in aquatic flowering plants, for which he originally received a grade of A+. Later, however, Prescott changed it to A−. For Howard, this was an unforgiving act, and he complains to this day about it.

When Howard arrived in Ann Arbor he discovered that the University of Michigan did not offer a program, not even a course, in plant pathology. He says

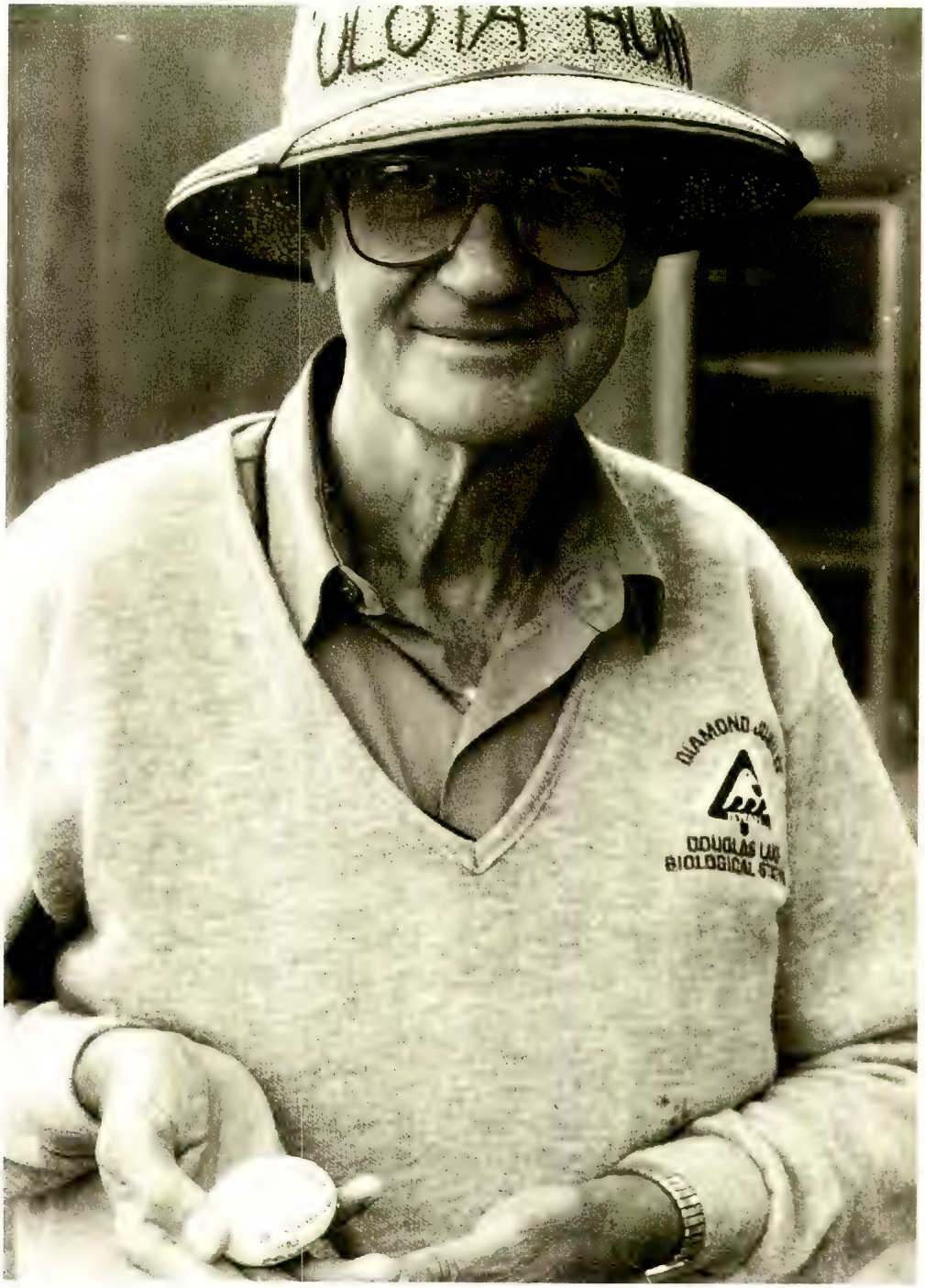


FIG. 13. Howard, the *Ulota* Hunter, University of Michigan Biological Station, summer, 1985. The hat was a birthday present from his class that year; the raw egg was received in the "mail."

eventually he "blundered into Steere," which was an "accident of fate." Of course, he would have known Steere from the previous summer's course in taxonomy at the Biological Station, so it probably didn't involve too much "blundering." In any event, he soon became interested almost exclusively in mosses and began his graduate work as Bill Steere's student.

He entered Michigan toward the end of a great period in bryology there under Steere's leadership. Steere attracted a host of students immediately before and after World War II. Howard was certainly the star of the group. Almost immediately he became interested in the moss flora of Mexico. Altogether, he made four collecting trips to Mexico and collected a large number of mosses. The experiences he gained on these trips expanded greatly his knowledge of tropical mosses and their ecology. He also visited the major herbaria of this country and compiled a wealth of distributional information. Jack Sharp tells with great delight that Howard came to the University of Tennessee to spend a week identifying Jack's collection. He was there almost a month, staying at the Sharps, whose home is called the "Sharp Motel" by bryologists. Howard had not known that Jack's unidentified material filled several large barrels. It was Howard who introduced the term "dung ball" to describe Jack's habit of collecting several handfuls of mosses, squeezing them all together and stuffing them, often in wet condition, into a paper bag or wrap them, unpressed, in folded newspapers.

Howard's thesis, "The Appalachian-Ozarkian Element in the Moss Flora of Mexico with a Check-list of All Known Mexican Mosses," was finished under Professor Harley H. Bartlett's ("Uncle Harley" as he was fondly known) direction because of Steere's departure for Stanford. Unfortunately, Howard's thesis was never published. It is undoubtedly the most-cited thesis in the history of bryology. A great deal of its substance was eventually lifted and included in one of Howard's more significant contributions, "The Geographic Origins of the Mosses of North America's Eastern Deciduous Forest," published in 1972, as a part of a symposium in Tokyo, which was held the previous year.

Howard's eleven years in Ottawa were very pleasant ones. He and Irene both loved the city, they had a nice home, albeit a bit small for an expanding family. She was a Canadian and "at home." While the National Museum was in antiquated quarters, there was generous financial support for technicians, equipment, and field work, and he lectured occasionally at Carleton University. He left an imprint on the National Museum that is well described in a letter from Wilf Schofield: "He built the bryological collection of the National Herbarium of Canada to world-class stature through active collecting and exchange. His organization of the collection and his great enrichment of the library are of profound significance to bryology."

Meanwhile, the bryology program at the University of Michigan became dormant after Steere's departure. In 1964, however, Rudolph M. Schuster was hired to revive the program, but, after a tumultuous year in Ann Arbor, Rudy departed for the University of Massachusetts. Howard was then offered the job. He couldn't resist the lure of his alma mater and accepted the offer of Associate Professor of Botany, beginning in the fall of 1965. He and Irene purchased a beautiful home in a very nice section of Ann Arbor where they still reside. Their years in Ann Arbor have undoubtedly been their happiest and most cherished. There the children grew up, married, and fledged. He became Curator and Professor in 1969 and served as Chairman of the Department of Botany from 1981–83, interrupted by a serious illness.

When he arrived in Ann Arbor, Howard quickly revived the graduate program

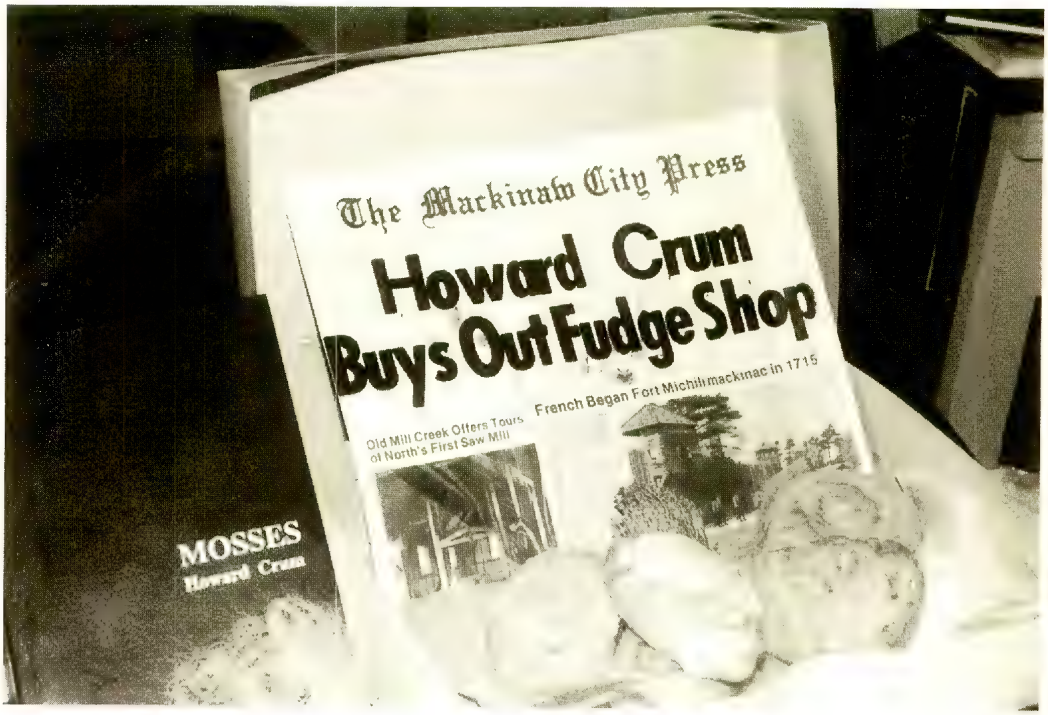

The Mackinaw City Press
Howard Crum Buys Out Fudge Shop
French Began Fort Michilimackinac in 1715
Old Mill Creek Offers Tours of North's First Saw Mill
MOSSES
Howard Crum

FIG. 14. Howard makes the front page news in Mackinaw City, summer, 1985.

in bryology and promptly set about revamping the quiescent bryophyte herbarium. Howard has supervised six Ph.D. students: Dale H. Vitt, 1970, now Professor of Botany at the University of Alberta, and currently President of the American Bryological and Lichenological Society and the International Association of Bryologists; William R. Buck, 1979, now Curator of Bryophytes at the New York Botanical Garden; Jeffrey W. Holcombe, 1980, now teaching in a private school in New England; Allan J. Fife, 1982, now on the staff of the Botany Division, Department of Scientific and Industrial Research, Christchurch, New Zealand; Jonathan Shaw, 1983, now Associate Professor of Biology at Ithaca College; and Joseph R. Rohrer, 1985, now Associate Professor of Biology at the University of Wisconsin-Eau Claire. Marie Cole was his only Masters student.

Howard's relations with his students were what they all describe as "hands-off." Following are some excerpts from a letter from Dale Vitt: "Howard always had time to talk, whether it was about bryology or just plain gossiping. From him I learned that there is only one way to be a good bryological taxonomist and that is to look at specimens. The more specimens one examines the better one will understand the species at hand. Surely no one else in the world has been able to name as many specimens from throughout the world as Howard. I rarely saw a specimen from really anywhere that he couldn't determine to genus and often a good guess to species."

Dale goes on to say: "I think Howard has been a remarkably efficient editor over the years (often without getting the credit that he deserved, e.g., the Flowers book). His thesis is surely one of the better ones to have been written at its time; it brought Mexican bryology into the 20th century. Although I don't agree with all his ideas, his 'Origins of Eastern North American mosses' paper is superbly written.

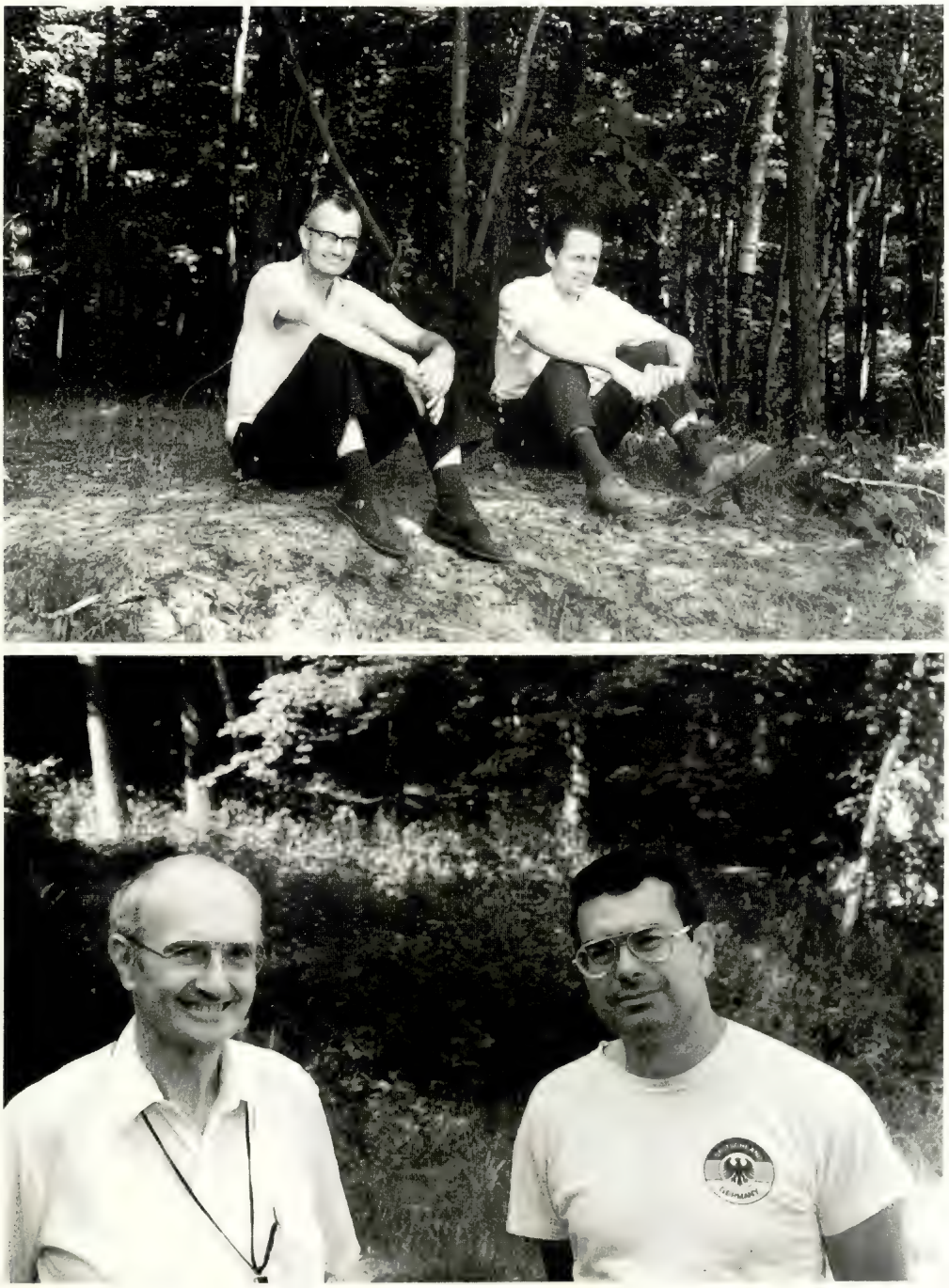


FIG. 15. Summer visitors at the Biological Station. Howard with Mason Hale in 1969 (above) and Dale Vitt in 1989 (below).

The Great Lakes Flora is a perfect flora down to the wonderful stories that it contains (including my favorite about Mungo Park). Of course your joint work couldn't be better!"

All his students emphasize his professionalism, which, with amazing success, he was able to pass along to them. Their published dissertations reflect this. He went

FIG. 16. Howard Crum with Bill Steere at the latter's 80th birthday celebration at the New York Botanical Garden, 4 November 1987.

through each thesis with a fine-toothed editorial comb. Individually, his relationship with his graduate students was mostly at the professional level, they tell me, but in a group he generally let his hair down and joined them in fun and clowning. Sometimes he surprised them with his "odd humor." Bill Buck tells of introducing his parents to Howard, who, after a studied look at them paused and remarked, to Bill's discomfort, "Well, you two look normal enough."

He was at his best at the Michigan Biological Station, where he still teaches every summer that health permits. Joe Rohrer describes his summer there as follows: "My fondest memories of Howard come from the summer of 1980, which I spent at Douglas Lake. I was to begin my doctoral work with him (at your sugges-

tion if you remember) that fall, and Howard strongly encouraged me to join him at the 'bug camp' for the summer so that I could get acquainted with him and the local bryophytes. He soon started calling me 'Jo Jo the Dog-faced Boy,' Howard has an odd sense of fun, but it also included poking fun at himself. For a class picture that summer, he allowed the students to adorn his shoulders with military-style macaroni of *Ptilium* and *Sphagnum*. The field trips that summer were great. We were in the field five or six days a week. Howard was famous for never neglecting to stop at a doughnut shop in the morning and often for ice cream in the afternoon. One student commemorated the experience in a song he titled the 'Bryophyte Blues.' One verse went:

> Drive all day and we don't stop
> Until we get to a donut shop,
> Buy a dozen, or maybe two
> And we hunt for mosses 'til the day is through."

In the summer of 1967, Howard invited Wolfgang Maass and me to the Biological Station for a month. Howard was teaching both bryology and lichenology with assistance from Norton Miller and Dick Harris. Dale Vitt was also there working on his dissertation. It was a great summer. I spent most of the time with cytological studies on mosses (still unpublished) and Maass and Howard spent a great amount of time collecting and arguing about *Sphagnum* concepts. We all had fun.

I had brought along a bottle of Howard's favorite bourbon and suggested that we file it away under the letter "B" for some wet and cold day. "No way," he said, and added that a year or so before a friend had brought him an expensive bottle of scotch and that they had filed it under "S" for that cold, rainy day. At an informal break in the bryology class Howard had told the students and others hanging around about some of Elizabeth G. Britton's interesting traits. She made a habit of swiping small samples of enticing specimens, including types, that she had borrowed, but she would always write across the original specimen in her large, familiar handwriting, "Took Piece." Soon, that cold rainy day arrived at the Station, and Howard went to the filing cabinet to retrieve the unopened bottle of scotch. To his amazement, it had been opened and was only three quarters full, but stuck to it was a slip of paper that, in a large handwritten scrawl, said "Took Piece." The "honest" culprit was never discovered.

The long tradition of bryology and lichenology at the Michigan Biological Station has been carried on most ably by Howard, and has to be listed as one of his major contributions to the field. He has made it a major training facility for bryology in this country. I encouraged all my students to go there and nearly all of them did so. Howard has invited colleagues and graduate students to use the Station as a base for their researches and in many instances he has obtained funds to support them.

Howard, at 69, is still teaching a rigorous field course at the Biological Station. Mary says ". . . . he is particularly proud of a nickname he acquired from his bryology students two years ago when they complained that they could not keep up with him in the field. These twenty year olds dubbed this 67 year old 'Hurricane Howard' and they called themselves the 'brood bodies.' We all have the class T-shirts to prove it!" Because the Crum children returned to the Station summer after summer, essentially through their entire childhood, it became a second home to them. They became a part of his professional and social life and were aquainted

FIG. 17. Bryophyte Reunion of the Summer Society honoring Howard Crum at the Biological Station, August, 1989. Above, Howard at his favorite thing, lecturing in a peat bog, Mackinac County, Michigan; and below, reminiscing with his first two Ph.D. students, Bill Buck (left) and Dale Vitt (right).

with students and colleagues. Mary says that at lunch one day a student told her "I just love groveling at the base of trees with your Dad. We shouldn't be getting credit for having this much fun."

Howard was a member of Bill Anderson's doctoral committee at Michigan. Bill

FIG. 18. The Bryophyte Reunion continues, August, 1989. Bill Buck, Lewis Anderson, Howard Crum, Grace Blanchard Iverson and Norton Miller (left to right).

wrote me the following. "One day I went to Howard and told him I wanted to change the subject of my dissertation. My first thesis was not working out well so I was switching to a problem that was sure to result in a publishable monograph in a reasonable time. Howard said, 'That's all very well, but what's going to be your gimmick in this new thesis?" 'My what?' 'Your gimmick. You know, the bit you'll use to convince the non-taxonomists on your committee that you did some science. Every taxonomist needs a gimmick, at least until he gets tenure.' I have remembered Howard's advice, made good use of it in my own career, and passed it along to my students. I have also borne in mind that while Howard cultivates the image of a vague and dithering sweetheart, he is actually a foxy strategist whose survival among the piranhas at the University of Michigan was not entirely a matter of good fortune."

Howard's contribution to Sphagnology is enormous. Completely self-taught, he approached the genus from an ecological vantage point. He soon recognized that Andrews' ultraconservative approach was an overreaction to Warnstorf's excessively narrow species concepts and did not mesh with what Crum saw in the field. On the other hand, he is troubled by more recent tendencies to edge back toward Warnstorfian attitudes, although some might call this edging forward. Howard has attempted to strike a middle ground in his concepts, although some can see his species concepts narrowing as his interests move into South America. Whatever, his North American treatise with its accurate descriptions and magnificent illustrations is the most useful work on *Sphagnum* that has been produced anywhere this century. He has set a standard that will be difficult to exceed.

I agree with Wilf Schofield, Dale Vitt, and just about everyone who has a copy, that his Great Lakes moss flora is a gem. As Wilf wrote me, it is ". . . a delight to read and browse for intriguing observations derived from a rich background of reading and [experiences] with living plants." All that is lacking is a comprehensive index to this huge cache of fascinating information. It is the only flora that I know of

that can be read with pleasure. It has and will continue to pique the interest of many a student, professional, and non-professional.

A habitual note-taker, Howard carries a notebook with him wherever he goes. He and I have collected together over much of the southeastern United States. I drove, of course, and he took notes. I think he wrote down every thought I had on the trips. "I didn't quite get that. Would you mind repeating it?" he would say. My copy of Grout's moss flora is so marked up with Howard's pencilings that I can scarcely use it. If he has a Bible, and I am sure he has, I would not be surprised if it is filled with marginal notes. If I send him a specimen that is somewhat unusual and doesn't quite fit a particular species, it comes back to me with a full penciled description which he jotted down while examining it. Once he sent me a description like this based on a *Sphagnum* that someone had sent him from Florida and that he thought was a new species. It proved to be ordinary *S. molle*. He had forgotten that there is a member of Section *Acutifolia* whose branch leaves have a resorption furrow. It is not often that he can be caught like this.

With the help of Bill Buck, Howard's published contributions to bryology are enumerated at the end of this article. Considering the seriousness and frequency of his illnesses they are nothing short of amazing. There are scarcely any breaks in the flow of publications through these years, indicating that he worked through and around his indispositions. He continues to work at the same pace. I can detect no let-up in quantity or quality of his output and there are still many more contributions to come.

I hesitate to attempt an assessment of Howard Crum's contribution to Bryology because I have a strong prejudice in his favor. Wilf Schofield, who has been one of Howard's associates over the years, has this to say: "I consider Howard to be one of the major bryologists of the 20th Century. He is intensely engaged in a fascination for bryophytes. I can attest that, once contracted, this condition is usually incurable. This commitment shows in his teaching, his lucid style of writing, and his sharing of his considerable knowledge through these potent means of communication." This says it well. Too, I think the scholarly qualities of his papers, reviews, and books, as well as those of his students, have set an example that has influenced bryology immensely, especially in North America.

His professional experience, services and awards are summarized below.

Instructor, Western Michigan College, 1946–47; Rackham State College Scholar, University of Michigan, 1947–48; Teaching Fellow, University of Michigan, 1948–49; Rackham Pre-Doctoral Fellow, 1949–51; Research Biologist and Acting Assistant Professor, Stanford University, 1951–53; Assistant Professor, University of Louisville, 1953–54; Research Assistant, Duke University, Summer 1954; American Bryological and Lichenological Society (Editor, *The Bryologist*, 1954–62, Associate Editor, 1962–76; President, 1962–63); Curator of Cryptogams, National Museum of Canada, 1954–65; Visiting Lecturer, University of Michigan Biological Station, Summer 1958; Lecturer, Carleton University, 1961–62; Curator, University Herbarium and Associate Professor of Botany, University of Michigan, 1965–69, Curator and Professor, 1969–present; Chairman, Department of Botany, University of Michigan, 1981–83; British Bryological Society (Associate Editor, *Journal of Bryology*, 1972–77); Academic Counselor, College of Literature, Science and Arts, University of Michigan, 1973–76, 77–present; Nordic Bryological Society; Southern Appalachian Botanical Club; Sigma Xi; Michigan Botanical Club (Board of Directors, 1977–84; Associate Editor, *The Michigan Botanist*, 1975–76, 85–present, Editor, 1977–84; President, Huron Valley Chapter, 1974–75); Editorial Board, *North American Flora*,

1985–present; Ruth M. Sinclair Memorial Award for Freshman-Sophomore Counseling, 1978; H. A. Gleason Award for Excellence in Botanical Publication, 1981 (presented to H. Crum and L. E. Anderson); Abstracting for *Excerpta Botanica* (1959–83); Convener for Bryological Foray and Sessions, IX International Botanical Congress, Montreal, 1959.

Crum! You bore me. I'm quitting.

ACKNOWLEDGMENTS

I am not sure that I can remember all the kind people that have helped me with this article. Because of the surprise element, I was not able to contact the best source of information, Howard Crum himself. I hope he will forgive errors. Foremost, I am indebted to William R. Buck. He has not only been a constant nag, his help with the bibliography greatly improved its accuracy and completeness and he has been a durable source of information and has helped in countless other ways. Irene Crum has provided me with a wealth of information that only she could supply. She has added greatly to the spice of the account. Bill Anderson kindly provided me with a copy of Howard's CV. The letters that Roger Crum, Mary Crum Scholtens, Bill Anderson, Joe Rohrer, Wilf Schofield, Jack Sharp, Jerry Snider, and Dale Vitt wrote me have been invaluable and their consent to be quoted is most appreciated. Pictures have been provided by Irene Crum, Mary Crum Scholtens, Bill Buck, Jerry Snider, and Dale Vitt. Finally, my wife, Pat, acted as chief censor, and Molly McMullen helped with the manuscript. I am grateful to both of them.

BIBLIOGRAPHY OF HOWARD A. CRUM

Compiled by Lewis E. Anderson and William R. Buck

1949

The discovery of fruiting *Gymnostomiella orcuttii* in Mexico. Bryologist 52(4): 208–211.

1950

Publication date of the Prodromus Bryologiae Mexicanae. Bryologist 53(1): 60, 61.

Additions to the moss flora of Panama. Bryologist 53(2): 139–152. (H. Crum and W. C. Steere)

Mosses from Honduras. Bryologist 53(4): 292–295.

Nota florística de una associación importante del suroeste de Tamaulipas, México. Bol. Soc. Bot. México 11: 1–4. (A. J. Sharp, E. Hernández X., H. Crum and W. B. Fox)

The Appalachian-Ozarkian element in the moss flora of Mexico with a check-list of all known Mexican mosses. Ph.D. Dissertation, University of Michigan, Ann Arbor. 504 pp.

Mosses of Baja California. Rev. Bryol. Lichénol. 19(3/4): 188–192. (L. F. Koch and H. Crum)

A checklist of the mosses of northeastern Mexico. Bol. Soc. Bot. México 12: 1–27.

A unique vegetational area in Tamaulipas. Bull. Torrey Bot. Club 78(6): 458–463. (E. Hernández X., H. Crum, W. B. Fox and A. J. Sharp)

1951

Notes on Mexican *Tayloriae*, with the description of a new species. Bryologist 54(4): 269–273.

1952

Bibliographic notes on Palisot de Beauvois' *Prodrome*. Bull. Torrey Bot. Club 79(5): 407–409.

Two new species of Mexican mosses collected by Aaron J. Sharp. Bryologist 55(1): 51–58.

Pseudosymblepharis in Middle America. Bryologist 55(2): 137–142.

A preliminary survey of the Nicaraguan moss flora. Bryologist 55(3): 159–165.

Mosses from Honduras. II. Bryologist 55(4): 279–285.

1953

The propagula of *Pterigynandrum filiforme*. Bryologist 56(2): 98–100.

Garckea phascoides in Panama. Bryologist 56(3): 204–207.

Additional bryophytes from Panama. Rev. Bryol. Lichénol. 22(3/4): 148–159. (H. Crum and C. B. Arzeni)

Otros musgos de Tamaulipas. Bol. Soc. Bot. México 15: 13–16. (H. Crum and A. J. Sharp)

1954

Additions to the moss flora of Kentucky. Trans. Kentucky Acad. Sci. 15(1/2): 24–26.
Mosses of Mexico. I. Species new to the country. Rev. Bryol. Lichénol. 23(3/4): 256–264.

1955

Taxonomic studies in the Funariaceae. Bryologist 58(1): 1–15. (H. Crum and L. E. Anderson)
Courses in bryology and lichenology to be offered during the summer of 1955. Bryologist 58(1): 78.
[Review of] Franz Schömmer: *Kryptogamen-Praktikum*. Bryologist 58(3): 260, 261.
Tayloria splachnoides and *T. acuminata* in America. Rev. Bryol. Lichénol. 24(3/4): 215–221.

1956

Syrrhopodon alatomarginatus. A new species from Trinidad. Trans. Brit. Bryol. Soc. 3(1): 72, 73.
Hedwig's *Species Muscorum* and its effective date of publication. Taxon 5(6): 130–133. (L. F. Koch and H. Crum)
Notes on *Hypnodon*, a genus of Orthotrichaceae. Bryologist 59(1): 26–34.
Two rare bryophytes new to Canada. Bryologist 59(1): 35.
[Review of] L. I. Savicz-Ljubitzkaja: *Musci frondosi (1). Sphagnales*. Bryologist 59(2): 148, 149.
[Review of] Harold Bastin: *Plants without flowers*. Bryologist 59(2): 149.
[Review of] G. M. Smith: *Cryptogamic botany. Volume II. Bryophytes and pteridophytes. Second edition*. Bryologist 59(2): 149, 150.
Two new species of *Barbula* (Musci) from the Southwest. Southw. Naturalist 1(1): 35–38.
Lindbergia brachyptera in North America. Bryologist 59(3): 203–212.
Puerto Rican Musci. New species and new combinations. Bryologist 59(4): 246–255. (H. Crum and W. C. Steere)
[Review of] E. Nyholm: *Illustrated moss flora of Fennoscandia, Fascicle II*. Bryologist 59(3): 226, 227.
[Review of] Josef Podpěra: *Conspectus Muscorum Europaeorum*. Bryologist 59(3): 227, 228.
Additional records of *Hypnodon perpusillus*. Bryologist 59(4): 255, 256.
[Review of] A. Boros: *Magyarország Mohái (Bryophyta Hungariae)*. Bryologist 59(4): 285.
Taxonomic studies on North American mosses. I–V. Jour. Elisha Mitchell Sci. Soc. 72(2): 276–291. (H. Crum and L. E. Anderson)
Additions to the moss flora of Kentucky. II. Trans. Kentucky Acad. Sci. 17(3/4): 131–134.
Bryophytes from Guadalupe Island, Baja California. Southw. Naturalist 1(3): 116–120. (H. Crum and H. A. Miller)

1957

A contribution to the moss flora of Ecuador. Svensk Bot. Tidskr. 51(1): 197–206.
Some additions to the California moss flora. Madroño 14(2): 74–79.
The Machris Brazilian Expedition. Botany: Musci. Los Angeles Co. Mus. Contr. Sci. 18: 1–8.
The mosses of Porto Rico and the Virgin Islands. N. Y. Acad. Sci. Scientific Surv. Porto Rico and the Virgin Islands 7(4): 396–599. (H. Crum and W. C. Steere)
[Review of] Arthur Jewell: *The observer's book of mosses and liverworts*. Bryologist 60(1): 47, 48.
[Review of] Sigfrid Arnell: *Illustrated moss flora of Fennoscandia. I. Hepaticae*. Bryologist 60(2): 166.
[Review of] H. S. Conard: *How to know the mosses and liverworts*. Bryologist 60(2): 166, 167.
[Review of] Henry A. Imshaug: *Catalogue of West Indian lichens*. Bryologist 60(4): 367.
[Review of] W. H. Welch: *Mosses of Indiana: an illustrated manual*. Bryologist 60(4): 367, 368.
[Review of] Z. Pávletic: *Prodromus flore briofita Jugoslavije*. Bryologist 60(4): 368.

1958

Canadian bryological notes. I. Bull. Natl. Mus. Canada 147: 116–123.
A contribution to the bryology of Haiti. Amer. Midl. Naturalist 60(1): 1–51. (H. Crum and W. C. Steere)
A survey of the moss flora of Jamaica. Bull. Inst. Jamaica, Sci. Ser. 8: 1–90. (H. Crum and E. B. Bartram)
Anacamptodon in North America. Bryologist 61(2): 136–140.
Taxonomic studies on North American mosses. VI–XIII. Jour. Elisha Mitchell Sci. Soc. 74(1): 31–40. (H. Crum and L. E. Anderson)
Some bryophytes from Baja California. Southw. Naturalist 3(1/6): 114–123. (H. Crum and W. C. Steere)

1959

Cytotaxonomic studies on mosses of the Canadian Rocky Mountains. Bull. Natl. Mus. Canada 160: 1–89. (L. E. Anderson and H. Crum)

The mosses of Gillam, Manitoba. Bull. Natl. Mus. Canada 160: 91–106. (H. Crum and W. B. Schofield)
Bryoceuthospora nom. nov. Bryologist 62(1): 66. (H. Crum and L. E. Anderson)
[Review of] J. J. Barkman: *Phytosociology and ecology of cryptogamic epiphytes.* Bryologist 62(1): 74.
[Review of] E. Nyholm: *Illustrated moss flora of Fennoscandia. II. Musci. Fasc. 3.* Bryologist 62(1): 75.
A contribution to the Jamaican moss flora. Bryologist: 62(3): 166–179.
A small collection of West Javanese mosses. Bryologist 62(3): 188–190.
[Review of] J. Szweykowski: *Prodromus florae hepaticarum Poloniae.* Bryologist 62(3): 195.
[Review of] C. C. Cunningham: *Forest flora of Canada.* Bryologist 62(3): 196.

1960

A bryological contribution from Florida. Bryologist 63(1): 32–46. (H. Crum and L. E. Anderson)
Bryophytes of the Mont Tremblant region. Bryologist 63(1): 59–63. (H. Crum and H. Williams)
Three new species of *Fissidens.* Bryologist 63(2): 93–98.
[Review of] Z. Pilous & J. Duda: *Klíč k určování mechorostů ČSR.* Bryologist 63(4): 255.
[Review of] B. Szafran: *Mchy (Musci).* Bryologist 63(4): 255.
[Review of] H. Weymar: *Buch der Moose.* Bryologist 63(4): 255.
[Review of] K. Bertsch: *Moosflora von Südwestdeutschland. Ed. 2.* Bryologist 63(4): 255, 256.
[Review of] W. B. Turrill, editor: *Vistas in botany.* Bryologist 63(4): 256.

1961

The vascular flora of Liard Hotsprings, B.C., with notes on some bryophytes. Bull. Natl. Mus. Canada 171: 131–197. (A. E. Porsild and H. Crum)
Luisierella barbula in Georgia. Bryologist 64(4): 315–320. (H. Crum and L. E. Anderson)
Mosses and liverworts of the Ottawa District—tentative list. December 1961. Department of Biology, Carleton University. 10 pp. mimeograph.
[Review of] E. Nyholm: *Illustrated moss flora of Fennoscandia. II. Musci. Fasc. 4.* Bryologist 64(4): 384, 385.
[Review of] S. Flowers: *The Hepaticae of Utah.* Bryologist 64(4): 385.
[Review of] L. F. Koch: *Bryology.* Bryologist 64(4): 385.
[Review of] W. H. Welch: *A monograph of the Fontinalaceae.* Bryologist 64(4): 385, 386.
A new *Fissidens* from Louisiana. Bryologist 64(4): 345–348. (H. Crum and L. E. Anderson)
A bryological contribution from Florida. II. Bryologist 64(4): 368–370. (H. Crum and L. E. Anderson)
[Review of] E. H. Walker: *A bibliography of eastern Asiatic botany. Supplement I.* Bryologist 64(4): 386.

1962

Mosses of the Douglas Lake region of northern Michigan. A Preliminary Survey. vii + 87 pp. mimeograph. University of Michigan.

1963

Encalypta brevicolla and *E. longicolla* in North America. Bull. Natl. Mus. Canada 186: 35–44.
Mosses previously unrecorded for Panama. Bryologist 66(2): 66–68. (W. H. Welch and H. Crum)

1964

Mosses of the Douglas Lake region of Michigan. Michigan Bot. 3(1/2): 3–12, 48–63.
[Review of] P. G. Taylor: *British ferns and mosses.* Bryologist 67(2): 241, 242.
[Review of] E. F. Warburg: *Census catalogue of British mosses. Ed. 3.* Bryologist 67(2): 242.
[Review of] B. R. Vashista: *Botany (for degree students). Part III. Bryophyta.* Bryologist 67(3): 382.
[Review of] [D. K. Zerov:] [*Flora of Hepaticae and Sphagnidae of the Ukraine.*] Bryologist 67(3): 382.
[Review of] P. A. Florschütz: *The mosses of Suriname. Part I.* Bryologist 67(3): 382, 383.
[Review of] Pang-Chieh Chen (chief compiler): *Genera Muscorum Sinicorum.* Bryologist 67(3): 383.
New names for some North American mosses. Bryologist 67(2): 162–164. (H. Crum, W. C. Steere and L. E. Anderson)
Notes on *Physcomitrium collenchymatum.* Bryologist 67(3): 350–355. (H. Crum and L. E. Anderson)

1965

James Kucyniak († March 11, 1962). Rev. Bryol. Lichénol. 33(3/4): 614–617, pl. XXVI.
Additions to the Douglas Lake bryoflora. Michigan Bot. 4(1): 26.
Hyophilopsis, a new genus of Pottiaceae. Bryologist 68(1): 68–71.
Mnium nudum in Japan. Bryologist 68(1): 118, 119.
Fissidens asplenioides new to the United States. Bryologist 68(1): 100–105. (H. Crum and L. E. Anderson)

The taxonomy and distribution of *Acaulon schimperianum*. Bryologist 68(2): 208–211. (H. Crum and L. E. Anderson)

A re-evaluation of *Glossadelphus andersonii*. Bryologist 68(2): 219, 220.

[Review of] R. S. Breen: *Mosses of Florida. An illustrated manual*. J. Hattori Bot. Lab. 28: 146.

Brotherella tenuirostris in Canada. Bryologist 68(2): 220, 221.

Grimmia trichophylla v. *indianensis* reviewed. Bryologist 68(2): 233–235.

New moss records from Haiti. Bryologist 68(2): 232, 233.

Refinements on the Jamaican bryoflora. Trans. Brit. Bryol. Soc. 4(5): 790–793.

Barbula johansenii, an arctic disjunct in the Canadian Rocky Mountains. Bryologist 68(3): 344, 345.

[Review of] F. H. Perring, P. D. Sell and S. M. Walters: *A flora of Cambridgeshire*. Bryologist 68(2): 271, 272.

[Review of] W. W. Judd & J. M. Speirs (eds.): *A naturalist's guide to Ontario*. Bryologist 68(2): 274, 275.

Barbula eustegia, a moss new to Canada. Canad. Field-Naturalist 79(2): 157.

Dicranella crispa, a moss new to eastern Canada. Canad. Field-Naturalist 79(3): 213.

A list of mosses of North America. Bryologist 68(4): 377–432. (H. Crum, W. C. Steere and L. E. Anderson)

Some additional new names for North American mosses. Bryologist 68(4): 432–434. (H. Crum, W. C. Steere and L. E. Anderson)

Hyophilopsis—a nomenclatural correction. Bryologist 68(4): 470.

[Review of] A. E. Jensen: *The how and why wonder book of mushrooms, ferns, and mosses*. Bryologist 68(4): 485.

1966

A tribute to Edwin B. Bartram. Bryologist 69(1): 124–134.

Evolutionary and phytogeographic patterns in the Canadian moss flora, pp. 28–42 *in* R. L. Taylor and R. A. Ludwig (eds.), *The evolution of Canada's flora*. Toronto.

The relationships of *Tetraplodon pennsylvanicus*. Bryologist 69(2): 205–207.

A note on the taxonomy and distribution of *Polytrichum ohioense*. Advancing Frontiers Pl. Sci. 17: 23–26.

Bryophytes of Labrador and Ungava. Bull. Natl. Mus. Canada 216: 87–101. (H. Crum and P. Kallio)

Bryophytes of Owen Sound and the Bruce Peninsula, Ontario. Bull. Natl. Mus. Canada 216: 102–122.

A taxonomic account of the genus *Thelia*. Bull. Natl. Mus. Canada 216: 123–127.

Bryophytes new to the Douglas Lake area. Michigan Bot. 5(2): 57–61. (N. G. Miller and H. Crum)

Edwin B. Bartram (1878–1964). Rev. Bryol. Lichénol. 34(3/4): 931–936.

1967

The status of *Hylocomium splendens* var. *tenue*. Bryologist 70(1): 78–101. (H. Crum and L. E. Anderson)

Studies in North American Bryaceae I–II. Bryologist 70(1): 106–110.

Three propaguliferous Pohlias from Michigan. Bryologist 70(1): 118, 119. (H. Crum and N. G. Miller)

Barbula malagana, a new species from Peru. Bryologist 70(2): 235–237.

A new species of *Pterigoneurum* from California. Madroño 19(3): 92–94.

A variety of *Timmia* (Musci) new to North America. Canad. Field-Naturalist 81(2): 113–115.

Bryophytes from the Upper Falls of the Tahquamenon. Michigan Bot. 6(2): 54–57. (H. Crum and N. G. Miller)

Fifty-six mosses new to Nicaragua. Bryologist 70(3): 365–369. (M. R. Crosby and H. Crum)

1968

Funaria flavicans, a moss new to Canada. Michigan Bot. 7(1): 24. (H. Crum and W. Botham)

Bryophytes new to Michigan. Michigan Bot. 7(3): 132–134. (H. Crum and N. G. Miller)

A new species of *Drummondia* from Mexico. Bryologist 71(2): 117–119. (D. H. Vitt and H. Crum)

Two new mosses from Hawaii. J. Hattori Bot. Lab. 31: 293–296. (H. Crum and D. Mueller-Dombois)

Mosses from Honduras. III. Advancing Frontiers Pl. Sci. 21: 189–193.

1969

Bryophytes new to Michigan. II. Michigan Bot. 8(1): 28, 29. (H. Crum and N. G. Miller)

A reconsideration of the relationship of *Barbula johansenii* (Musci). Canad. Field-Naturalist 83(2): 156, 157.

Nomenclatural notes on North American mosses. Bryologist 72(2): 240–246.

Recent cryptogamic collections in Barbados. J. Barbados Mus. & Hist. Soc. 33: 86, 87. (W. H. Welch and H. Crum)

1970

Sphagnum in Charlevoix County, Michigan. Michigan Bot. 9(2): 114–116. (W. Zales and H. Crum)
Mosses new to the flora of Michigan. Michigan Bot. 9(2): 139–141.
Groutiella tomentosa new to the United States. Bryologist 73(1): 145–149. (D. H. Vitt and H. Crum)
A new species of *Cryphaea* from Florida. Bryologist 73(2): 380, 381.
Recent cryptogamic collections in the West Indies. Rev. Bryol. Lichénol. 37(2): 223–235. (W. H. Welch and H. Crum)

1971

Brachymenium andersonii, a new species. Bryologist 74(1): 47–49.
Nomenclatural changes in the Musci. Bryologist 74(2): 165–174.
"*Leucodon sciuroides*" in North America. Bryologist 74(3): 373, 374. (H. Crum and L. E. Anderson)
Three new moss species from the Hawaiian Islands. Bryologist 74(4): 484–489. (W. J. Hoe and H. Crum)

1972

The geographic origins of the mosses of North America's eastern deciduous forest. J. Hattori Bot. Lab. 35: 269–298.
Validation of *Leucodon brachypus* var. *andrewsianus*. Bryologist 75(1): 101. (H. Crum and L. E. Anderson)
Mosses new to the state of Michigan. Michigan Bot. 11(3): 123, 124.
Mosses of unusual interest from Baja California. Madroño 21(6): 403, 404.
A taxonomic account of the Erpodiaceae. Nova Hedwigia 23(2+3): 201–224.
Sphagnum magellanicum new to the West Indies. Bryologist 75(3): 359, 360. (H. Crum and F. J. Hermann)
A new *Desmatodon* from Virginia. Bryologist 75(3): 360–362.
The dubius origin of *Glyphomitrium canadense* Mitt. J. Bryol. 7(2): 165–168.
Splachnum ampullaceum in West Virginia. Castanea 37(4): 253–257. (H. Crum, E. G. Fisher and H. C. Burtt)
[Review of] E. Lawton: *Moss Flora of the Pacific Northwest*. Bryologist 75(2): 205–207.
Disjunctions in bryophytes. Ann. Missouri Bot. Gard. 59(2): 174–204.

1973

Leucobryum albidum new to Michigan. Michigan Bot. 12(2): 117.
A new list of mosses of North America north of Mexico. Bryologist 76(1): 85–130. (H. Crum, W. C. Steere and L. E. Anderson)
Mosses of the Great Lakes Forest. Contr. Univ. Michigan Herb. 10: 1–404.
[Review of] J. Taylor and A. P. Underhill: *Liverworts, a photographic study*. Bryologist 76(4): 590, 591.

1974

Dicranum muehlenbeckii, a moss newly discovered in Michigan. Michigan Bot. 13(2): 64.
A new *Grimmia* from Michigan's Upper Peninsula. Michigan Bot. 13(4): 171–174.
[Review of] O. Degener, I. Degener and H. Hörmann: *Mosses of Hawaii*. Bryologist 77(1): 103.
Some bryophytes of Silumiut Island, Northwest Territories. Canad. Field-Naturalist 88(3): 361, 362. (N. McCarthy and H. Crum)
A new *Sphagnum* from high altitude Costa Rica. Ann. Missouri Bot. Gard. 61(3): 904–906. (H. Crum and M. R. Crosby)

1975

The vertical zonation of *Sphagnum* species in hummock-hollow complexes in northern Michigan. Michigan Bot. 14(4): 190–200. (D. H. Vitt, H. Crum and J. A. Snider)
Notes on the distribution of *Sphagnum tenellum*. Contr. Univ. Michigan Herb. 11(2): 85–87.
Comments on *Sphagnum capillaceum*. Contr. Univ. Michigan Herb. 11(2): 89–93.
Seligeria tristichoides, a moss new to the West. Canad. Field-Naturalist 89(3): 317, 318.

1976

Mosses of the Great Lakes Forest. Rev. ed. University of Michigan Herbarium, Ann Arbor. 404 pp.
Distribution of *Grimmia cribrosa* in North America. Bryologist 79(3): 355–357. (R. R. Ireland and H. Crum)
Revision of the genus *Rozea* (Musci). Bryologist 79(4): 406–421. (W. R. Buck and H. Crum)

Sphagnum taxa and their distribution in Iowa. Proc. Iowa Acad. Sci. 83(3): 98–101. (H. Crum, N. R. Lersten and G. H. Crum)

1977

William Campbell Steere. Bryologist 80(1): 1.

Grimmia pulvinata in eastern North America. Bryologist 80(1): 152, 153. (H. Crum and Y. Mescall)

[Review of] A. Boros and M. Jarai-Kornlódi: *An atlas of recent European moss spores*. Rev. Palaeobot. Palynol. 23(5): 404–406.

Sphagnum quinquefarium in the American West. Bryologist 80(1): 156–158. (H. Crum and J. A. Snider)

Meiothecium, a new record for North America. Bryologist 80(1): 188–193.

New combinations and new taxa of mosses proposed by Nils Conrad Kindberg. Mem. New York Bot. Gard. 28(2): 1–220. (W. C. Steere and H. Crum)

Proposal for the conservation of *Pleurozium* Mitt. Taxon 26(5/6): 596, 597. (M. R. Crosby and H. Crum)

Desmatodon steereanus, a new species of Pottiaceae from Peru. Bryologist 80(4): 638–640. (R. H. Zander and H. Crum)

William Campbell Steere. An account of his life and work. Bryologist 80(4): 662–694.

1978

Sphagnum richardsianum, a new species from Mexico. Contr. Univ. Michigan Herb. 11(5): 281–283.

Entodon schleicheri new to North America. Bryologist 81(3): 429–432. (W. R. Buck and H. Crum)

A re-interpretation of the Fabroniaceae with notes on selected genera. J. Hattori Bot. Lab. 44: 347–369. (W. R. Buck and H. Crum)

Alexander William Evans. *In:* C. C. Gillispie (ed. in chief), *Dictionary of Scientific Biography* 15(Suppl. 1): 148–151. Charles Scribner's Sons, New York.

1979

An expanded description of *Sphagnum splendens*. Michigan Bot. 18(2): 69–72.

Donrichardsia, a new genus of Amblystegiaceae (Musci). Fieldiana, Bot., n.s. 1: 1–18. (H. Crum and L. E. Anderson)

Tortula ammonsiana, a new species from West Virginia. Bryologist 82(3): 469–472. (H. Crum and L. E. Anderson)

1980

A guide to the identification of Mexican *Sphagna*. Contr. Univ. Michigan Herb. 14: 24–52.

Comments on *Sphagnum henryense*. Contr. Univ. Michigan Herb. 14: 53–56.

Mosses of North America. [Exsiccati and Schedae.] Fasc. I–IV. Nos. 1–200. University of Michigan and Duke University. (H. Crum and L. E. Anderson)

1981

Mosses of eastern North America. Vols. 1 and 2. 1328 pp. Columbia University Press, New York. (H. Crum and L. E. Anderson)

Mosses of North America. [Exsiccati and Schedae.] Fasc. V–X. Nos. 201–500. University of Michigan and Duke University. (H. Crum and L. E. Anderson)

An inventory of John Macoun's *Canadian Musci*. Occ. Pap. Farlow Herb. 16: 13–36.

Taxonomic and nomenclatural notes on Middle American mosses. Bryologist 84(3): 390–393.

Philonotis corticata, new from Mexico. Bryologist 84(3): 398–401. (H. Crum and D. Griffin, III)

Eccremidium, a genus of Ditrichaceae new to the Americas. Bryologist 84(4): 527–532.

Joyce Hedrick Jones (U.S.A.): 1897–1980. Internatl. Lichenol. Newsl. 14(2): 15, 16.

1982

Bryophyta. *In:* S. P. Parker, *Synopsis and classification of living organisms* 1: 272. McGraw-Hill, New York.

Mosses Musci. Pages 525–527; Liverworts and hornworts Hepaticae and Anthocerotae. Page 527; Lichens Lichenes. Pages 532, 533. *In:* S. J. Wernert (ed.), *Reader's Digest American wildlife*. Pleasantville, New York.

Comments on the Mielichhoferioideae of Central America with the description of a new species of *Synthetodontium*. Contr. Univ. Michigan Herb. 15: 209–217. (A. J. Shaw and H. Crum)

Mosses of North America. [Exsiccati and schedae.] Fasc. XI–XIV. Nos. 501–700. University of Michigan and Duke University. (H. Crum and L. E. Anderson)

1983

Grimmia hermannii, new to Canada. Michigan Bot. 22(1): 10.

Mosses of the Great Lakes Forest. Ed. 3. University of Michigan Herbarium, Ann Arbor. 417 pp.

Diagnoses of the new species [in part]. *In:* K. Mägdefrau, The bryophyte vegetation of the forests and paramos of Venezuela and Colombia. Nova Hedwigia 38: 54, 56–61.

[Review of] H. Godwin: *The archives of peat bogs.* Bryologist 86(4): 402, 403.

Mosses of North America. [Exsiccati and schedae.] Fasc. XV–XX. Nos. 701–1000. University of Michigan and Duke University. (H. Crum and L. E. Anderson)

1984

Vegetative reproduction in *Platydictya.* Michigan Bot. 23(1): 21, 22.

Crassicosta, a new genus of Amblystegiaceae from northern Mexico. Bryologist 87(2): 149, 150. (H. Crum and A. J. Sharp)

Fossombronia in Michigan. Michigan Bot. 23(4): 157–163. (N. G. Miller and H. Crum)

Notes on tropical American mosses. Bryologist 87(3): 203–216.

New and interesting mosses from Costa Rica. J. Bryol. 13(2): 193–200. (H. Crum and P. W. Richards)

Two new species of *Sphagnum* from Costa Rica. Cryptogamie, Bryol. Lichénol. 5(3): 293–297.

Acaulon casasianum, a new species from Spain. Lindbergia 10(1): 1–3. (M. Brugués and H. Crum)

Sphagnopsida. Sphagnaceae. No. Amer. Fl. ser. II, 11: 1–180.

Peristome homology in *Mielichhoferia* and a taxonomic account of North American species. J. Hattori Bot. Lab. 57: 363–381. (J. Shaw and H. Crum)

Schistidium obtusifolium, a new species of the Grimmiaceae from Quebec. Bryologist 87(4): 371–373. (R. R. Ireland and H. Crum)

[Review of] W. D. Reese: *Mosses of the Gulf South. From the Rio Grande to the Apalachicola.* Bryologist 87(3): 287, 288.

1985

Lewis Anderson, a tribute from a friend and colleague. Monogr. Syst. Bot. Missouri Bot. Gard. 11: 1–27.

Two undescribed species of *Hygrohypnum* from Mexico. Bryologist 88(1): 22, 23.

A new genus of Hookeriaceae from Mexico. Bryologist 88(1): 23, 24.

Notes on *Pylaisiadelpha* in Mexico. Bryologist 88(1): 27, 28.

New *Sphagna* from Brazil. Cryptogamie, Bryol. Lichénol. 6(2): 181–184.

Traditional make-do taxonomy. Bryologist 88(3): 221, 222.

Pseudoleskeella papillosa, a rare moss in Quebec. Bryologist 88(4): 357, 358.

1986

A survey of the moss genus *Sclerodontium.* Hikobia 9(4): 289–295.

Fossombronia and the mystery of spore dispersals. Michigan Bot. 25(3): 120–122.

Sphagnaceae. *In:* G. S. Mogensen (ed.), Illustrated moss flora of arctic North America and Greenland. Meddel. Grønland, Biosci. 18(2): 3–61.

Taxonomic and nomenclatural addenda to the Mexican moss flora. Bryologist 89(1): 23–27.

1987

A new section and species of *Sphagnum* from Ecuador. Contr. Univ. Michigan Herb. 16: 141–143.

Some Latin American mosses new to science. Contr. Univ. Michigan Herb. 16: 135–140.

Bestia, Tripterocladium, and *Isothecium:* an explication of relationships. Bryologist 90(1): 40–42.

New species of *Sphagnum* from South America. J. Hattori Bot. Lab. 63: 77–97.

Leratia and its place in the Orthotrichaceae, subfamily Macromitrioideae. Mem. New York Bot. Gard. 45: 602–608.

1988

A focus on peatlands and peat mosses. University of Michigan Press, Ann Arbor. xi + 306 pp. (H. Crum in collaboration with S. Planisek)

A new species of *Aulacopilum* from Brazil. Bryologist 91(3): 191, 192.

[Review of] R. R. Ireland and G. Bellolio-Trucco: *Illustrated guide to some hornworts, liverworts and mosses of eastern Canada.* Bryologist 91(3): 250.

[Review of] E. Nyholm: *Illustrated flora of Nordic mosses. Fasc. I. Fissidentaceae–Seligeriaceae.* Bryologist 91(3): 250.

A contribution to the *Sphagnum* (Sphagnaceae) flora of Paraguay. Brittonia 40(2): 188–194. (H. Crum and W. R. Buck)

1989

Noteworthy collections. Michigan. *Sphagnum obtusum* Warnst. (Sphagnaceae). Michigan Bot. 28(1): 38.

Notes on South American species of *Sphagnum*. J. Bryol. 15: 531–536.

New tropical American species of *Sphagnum*. Bryologist 92(1): 98–104.

William Campbell Steere (1907–1989). Michigan Bot. 28(2): 58.

Long live the lichens. Michigan Nat. Resources Mag. 55(5): 22–26.

New names for some North American mosses. Bryologist 92(4): 533. (H. Crum and L. E. Anderson)

1990

An evaluation of familial limits among the genera traditionally aligned with the Thuidiaceae and Leskeaceae. Contr. Univ. Michigan Herb. 17: 55–69. (W. R. Buck and H. Crum)

Comments on *Sphagnum* sect. *Sphagnum* in South America. Contr. Univ. Michigan Herb. 17: 71–81.

A new look at *Sphagnum* sect. *Acutifolia* in South America. Contr. Univ. Michigan Herb. 17: 83–91.

Preliminary notes on *Sphagnum* sect. *Subsecunda* in South America. Contr. Univ. Michigan Herb. 17: 93–97.

Noteworthy collections. Michigan. *Funaria flavicans* Michaux (Funariaceae). Michigan Bot. 29(1): 27.

Sphagnum (*Subsecunda*) *boomii* Crum, n. sp. *In:* W. R. Buck, Contributions to the moss flora of Guyana. Mem. New York Bot. Gard. 64: 185, 186.

Sphagnum inretortum, a new species in a new section from Bolivia. Bryologist 93(3): 283–285.

List of the mosses of North America north of Mexico. Bryologist 93(4): 448–499. (L. E. Anderson, H. Crum and W. R. Buck)

1991

Two new species of *Sphagnum* from Brazil. Bryologist 94(3): 301–303.

Liverworts and hornworts of southern Michigan. University of Michigan Herbarium, Ann Arbor. vii + 233 pp.

A partial clarification of the Lembophyllaceae. J. Hattori Bot. Lab. 69: 313–322.

Riccia frostii, a liverwort new to Michigan. Michigan Bot. 30(1): 15–21. (M. R. Penskar, N. G. Miller and H. Crum)

Contr. Univ. Mich. Herb. 18:39–41. 1992.

CRUMUSCUS VITALIS GEN. ET SP. NOV. (DITRICHACEAE)

William R. Buck
New York Botanical Garden
Bronx, NY 10458-5126, U.S.A.

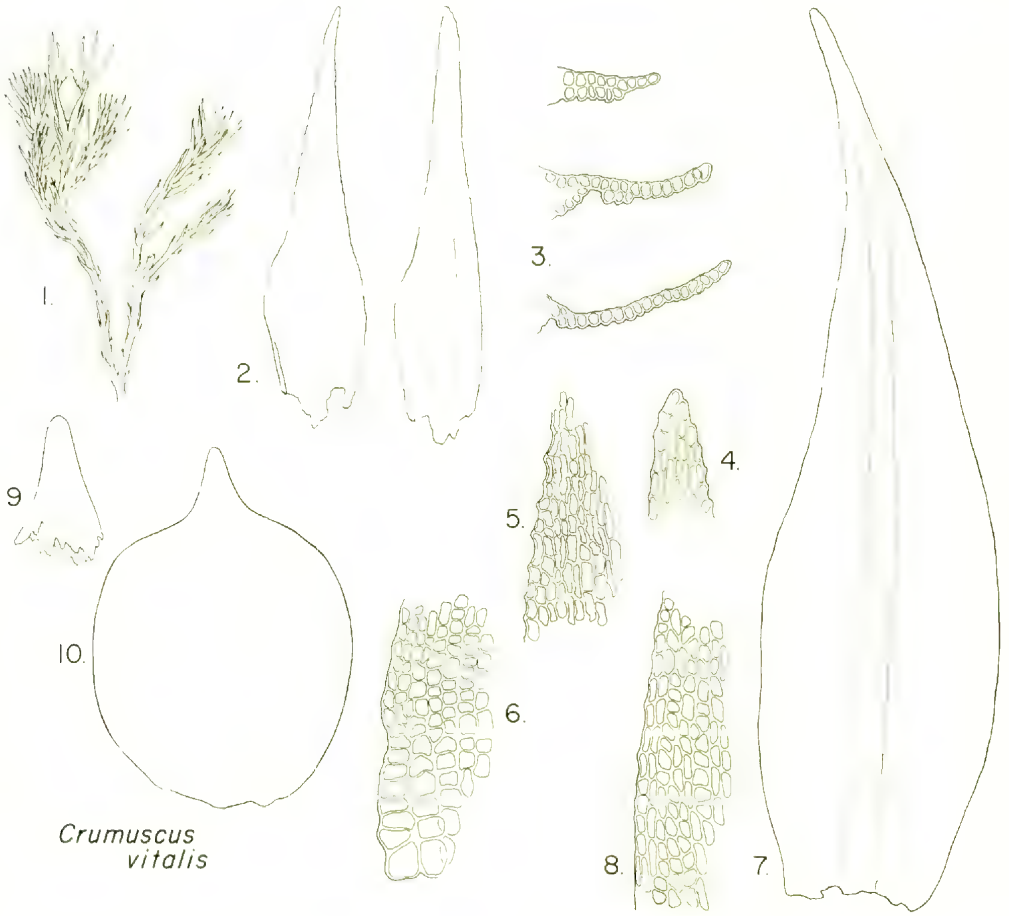
Jerry A. Snider
Department of Biological Sciences
University of Cincinnati
Cincinnati, OH 45221-0006, U.S.A.

In 1982, Daniel M. Vital of the Instituto de Botânica in São Paulo, Brazil, sent around duplicates of a ditrichaceous moss he had collected on Itatiaia five years earlier. After receiving no responses, he sent it to W.R.B. several years later, who also let it languish for a few years before facing up to it. After some discussion on its affinities to *Pleuridium*, we have decided to describe it as a new genus. Both of us have had close and amiable ties to Howard Crum for many years and are delighted to have this opportunity to describe a distinctive new genus for a good friend and colleague.

Crumuscus vitalis Buck & Snider, gen. et sp. nov. FIGS. 1–10.

A *Pleuridio* foliis perichaetialibus a caeteris valde absimilibus, cellulis folii distaliter bistratosis mamilloso-prorulosis necnon calyptris mitriformibus differt.

Plants perennial, very small, to ca. 8 mm tall but often leafy only in upper 2–3 mm with old, denuded stems buried in soil. Stems reddish, especially with age, branching from beneath perichaetia and thus obscuring them, ca. 100 μm in diameter, in cross-section with ca. 7 layers of small, firm-walled cells surrounding a well developed central strand of very small, thin- and fragile-walled, collenchymatous cells; rhizoids smooth; axillary hairs 28–45 μm long, 2-celled, with a single, short to elongate, brown basal cell and a single, elongate, hyaline apical cell. Leaves when dry erect, often ± falcate, obscurely homomallous, when moist remaining erect but neither falcate nor homomallous, becoming larger toward stem apices, oblong-lanceolate, sometimes broadly so, ca. 0.6–0.9 mm long, broadly long-acuminate from an expanded base; margins subentire to crenulate, plane; costa broad and strong, ca. 40–55 μm wide at base, almost filling the acumen, excurrent, roughened above at back from projecting cell ends, in cross-section with 4 guide cells and two bands of stereids; laminal cells bistratose above (except at extreme margins), at shoulders unistratose with bistratose streaks, unistratose below, mostly rectangular, (1–)2–5:1, (9–)11–22 μm long, firm-walled, mammillose-prorulose at back above, smooth below, scarcely differentiated at insertion. Paroicous? Perichaetia terminal, leaves strongly and rather abruptly differentiated, erect, lanceolate to broadly lanceolate, to 2.5 mm long, concave, gradually acuminate; margins entire, plane to irregularly narrowly recurved; costa subpercurrent to percurrent, not filling the acumen, roughened at back; cells unistratose except perhaps in extreme acumen, quadrate to short-rectangular above, long-rectangular below, smooth. Setae very short, ca. 0.1 mm long, brittle, smooth, from a naked vaginula ca. 0.45 mm long; capsules immersed, cleistocarpous, eperistomate, spherical to ovoid, stoutly apicu-



FIGS. 1–10. *Crumuscus vitalis*. 1. Habit, ×8. 2. Vegetative leaves, ×50. Laminal cross-sections (from top to bottom) near leaf apex, at leaf shoulder, near leaf base, ×200. 4. Leaf apex, ×200. 5. Upper laminal cells at margin, ×200. 6. Lower laminal cells at margin, ×200. 7. Perichaetial leaf, ×50. 8. Lower marginal perichaetial leaf cells, ×200. 9. Calyptra, ×50. 10. Detached capsule, ×50. Figs. 1–6, 9, 10 from the type (NY); figs. 7, 8 from *Schäfer-Verwimp & Verwimp 14639* (NY).

late, 0.75–0.85 mm long including the 0.15–0.2 mm long apiculus, separating from the seta at base of the capsule; exothecial cells irregularly rectangular, firm-walled, becoming gradually shorter and quadrate toward the apiculus; stomata none. Spores ± spherical, tardily separating from tetrads, 17–20 μm in diameter, papillose to verruculose. Calyptrae mitrate, minute, covering scarcely more than the capsular apiculus, 0.25–0.3 mm long, naked, smooth or slightly roughened.

TYPE. BRAZIL. Rio de Janeiro: Parque Nacional de Itatiaia, ca. 3 km SW of Pico das Agulhas Negras, 23°23′S, 44°38′W, on rocky cliff covered with thin layer of soil, 24 July 1977, *D. M. Vital 7435* (NY!, holotype; BUF, CINC!, FLAS, MO, SP!, isotypes).

ADDITIONAL SPECIMEN SEEN. BRAZIL. Minas Gerais: Nationalpark Itatiaia, auf feuchtem, offenen Humus nahe Brejo da Lapa, 2120 m, 7 July 1991, *Schäfer-Verwimp & Verwimp 14639* (NY).

This new genus of Ditrichaceae is named in honor of Howard Crum on the occasion of his 70th birthday; we are pleased to have come up with a name that is

not crummy-sounding! The specific epithet honors the collector, Daniel Moreira Vital, now a vital 67.

Crumuscus is closely related to *Pleuridium* as evidenced by capsule morphology and leaf areolation. It differs from *Pleuridium* on the basis of the following: the lack of stomata in the capsule wall, the mitrate calyptrae, the bistratose and mammillose-prorulose upper lamina of the vegetative leaves, and the leaf costa showing four guide cells and two stereid bands in transverse section.

Crumuscus appears to approach *Pleuridium* through *P. lindigianum* (Hampe) Churchill. The latter usually lacks stomata in the capsule wall and has mitrate calyptrae. However, the leafy gametophyte is typically that of *Pleuridium* in having unistratose, smooth leaf cells and undifferentiated, sub-stereid cells in the costal cross-section. Differentiated guide cells and stereid bands are absent. *Pleuridium papillosum* Magill, a species endemic to South Africa, is the only known *Pleuridium* to exhibit papillose leaf cells. In the latter, however, the unistratose laminal cells have several low, blunt papillae over the lumina. Additionally, the capsules contain stomata, and the calyptrae are cucullate.

Crumuscus appears to be even more closely aligned to the geographically sympatric *Cladastomum,* a genus both poorly known and collected. This genus, of two species (and a dubious variety), is confined to the Agulhas Negras region of Itatiaia National Park and Pico da Bandeira of Caparaó National Park, both part of the Serra da Mantequeira in eastern Brazil. The two genera share the following features: mitrate calyptrae, capsules lacking stomata, stems with a well developed central strand, and leaf costae in cross-section showing guide cells surrounded above and below by stereid bands. However, *Cladastomum* differs from *Crumuscus* in its overall aspect of julaceous sterile shoots, its ovate-cuspidate leaves appressed to the stems, as well as its production of faintly bipolar spores.

ACKNOWLEDGMENTS

We are grateful to the collectors of the material, Daniel Vital and Alfons Schäfer-Verwimp (really his wife Inge), for making it available to us, and for accompanying the senior author to Parque Nacional Itatiaia, where, in addition to the Schäfer-Verwimp collection of *Crumuscus, Cladastomum* was also collected. Rupert Barneby graciously corrected the Latin diagnosis, and Bobbi Angell prepared the elegant illustration.

Contr. Univ. Mich. Herb. 18:43–71. 1992.

KEY TO THE MOSS GENERA OF NORTH AMERICA NORTH OF MEXICO

Dale H. Vitt
Department of Botany
University of Alberta
Edmonton, Alberta T6G 2E9, Canada

William R. Buck
New York Botanical Garden
Bronx, NY 10458-5126, U.S.A.

Traditionally, mosses have been considered by many to present severe difficulties in identification of both species and genera. However, often if the genus is known, species identification follows with much less difficulty. Moreover, most regional moss floras present keys to species beginning at either the family or genus rank. We present here a key to the genera of mosses found in North America, north of Mexico. The key is strictly dichotomous and attempts were made to use gametophytic features whenever possible.

Mosses (Class Bryopsida or Musci) are the largest group of plants in the Bryophyta, and are the third largest class of green land plants in North America following the Monocots and Dicots. The recently published lists of North American mosses (Anderson *et al.* 1990 [Andreaeidae and Bryidae]; Anderson 1990 [Sphagnidae]) tabulate 1320 species in 312 genera. To these, we add the genus *Takakia* with two species (Murray 1988; Smith *et al.* 1990). Within the 313 genera of mosses found in North America, 15 have 15 or more species. Only two genera have more than 50 species—*Sphagnum* with 72 and *Bryum* with 66; five genera have 30 or species (*Orthotrichum*—37, *Fissidens*—36, *Grimmia* and *Brachythecium* each with 34, and *Pohlia*—30). Other large genera are *Tortula* (29), *Dicranum* (27), *Racomitrium* (24), *Hypnum* (21), *Campylopus* (18), *Hygrohypnum* (18), *Encalypta* (16), and *Polytrichum* (15). These 15 genera contain 476 or 36% of the North American species.

Historically, keys to mosses have used growth form (acrocarpy *vs.* pleurocarpy) as a major dichotomy. We have resisted the use of this character whenever possible, and instead placed more emphasis on microscopic features of the leaves; namely the presence, absence and number of costae found on leaves and on the ornamentation of leaf cells (papillose *vs.* smooth).

Generic concepts depend largely on previous monographic work completed in particular families. Some North American families have had no recent generic revision, while others have newly revised generic concepts in place. We have followed the generic concepts presented in Anderson *et al.* (1990), including the recognition of segregate genera in the Mniaceae, Amblystegiaceae, and Grimmiaceae. These generic concepts differ somewhat from those accepted in the Canadian (Ireland *et al.* 1987) and European checklists (Corley *et al.* 1981).

Reprints of this article may be purchased from the American Bryological and Lichenological Society. Send orders to Jerry A. Snider, Dept. of Biological Sciences, University of Cincinnati, Cincinnati, OH 45221–0006, U.S.A.

Floristic treatments of North American mosses are available for many areas of the continent, and date back to the 1880's when Lesquereux and James (1884) published the first treatment of mosses of the continent. Still a valuable source of information and the only flora that treats the southwestern United States is Grout's *Moss Flora of North America* (Grout 1931–40). In more recent times (since 1970) several excellent regional floras have been written and form the basis of our understanding of North American mosses. Included are the following manuals: Eastern North America—Crum and Anderson (1981); the United States Pacific Northwest—Lawton (1971); Utah—Flowers (1973); northern Michigan—Crum (1973); Maritime Provinces of Canada—Ireland (1982); the southeastern Gulf Shore—Reese (1984); the Interior Highlands—Redfearn (1983); and northwestern North America—Vitt *et al.* (1988). Definition of terms used in this key follow those given in Crum and Anderson (1981) and in Magill (1990).

We have the great privilege to dedicate this key to Howard Crum, our teacher and good friend. His patience and perseverence in performing the unenviable task of teaching both of us the fundamentals of science and bryology are remarkable. Without him, neither of us would have been able to complete the present work. To Howard Crum we give our heartfelt thanks.

1. Gametophytes seemingly absent (consisting only of protonemata); sporophytes of asymmetric capsules and papillose setae ..... *Buxbaumia*
1. Gametophytes present (with obvious leaves); sporophytes various 2
   2. Leaf cells arranged in a network of narrow, green cells alternating with large hyaline cells; branches usually in clusters ..... *Sphagnum*
   2. Leaf cells of one kind (green), or if of two kinds, branches never in clusters 3
3. Leaves attached in two rows on opposite sides of the stem (distichous) 4
3. Leaves attached all around the stem (foliate stems sometimes flattened [complanate]) 7
   4. Leaves appearing split at the base, consisting of two vaginant laminae which clasp the stem and base of the leaf above (equitant) ..... *Fissidens*
   4. Leaves with expanded bases, not clasping leaf above 5
5. Leaves ecostate; protonemata luminous ..... *Schistostega*
5. Leaves unicostate; protonemata not luminous 6
   6. All leaves with a rough (papillose), linear subula ..... *Distichium*
   6. Vegetative leaves with a smooth mucro; perichaetial leaves with a smooth subula ..... *Bryoxiphium*
7. Leaves with lamellae or filaments on the adaxial (upper) surface of the costa (excluding propagula) 8
7. Leaves without lamellae or filaments on the adaxial surface of the costa (but propagula sometimes present) 23
   8. Leaves with filaments on the adaxial surface of the costa 9
   8. Leaves with lamellae on the adaxial surface of the costa 10
9. Leaf margins broadly inrolled (and mostly obscuring the filaments) ..... *Aloina*
9. Leaf margins reflexed to revolute ..... *Crossidium*
   10. Leaves bordered with elongate cells ..... *Atrichum*
   10. Leaves without elongate, marginal cells 11
11. Leaves ciliate at upper part of hyaline sheath ..... *Bartramiopsis*
11. Leaves eciliate 12

12. Upper leaf margins bistratose with paired, multicellular teeth; leaf apices with slender, smooth, caducous awns; restricted to the arctic ..... *Lyellia*
12. Upper leaf margins unistratose with single teeth or entire; leaf apices muticous or with serrate awns 13
13. Lamellae 2–4; leaves hyaline awned; plants small, less than 5 mm; peristome none or rudimentary and fragile ..... *Pterygoneurum*
13. Lamellae 4–50; leaves mostly not awned; plants mostly larger; peristome of 32 or 64 persistent teeth 14
14. Lamellae distinctly wavy 15
14. Lamellae straight 16
15. Upper leaf margins with border of hyaline, short-rhombic cells ..... *Psilopilum*
15. Upper leaf margins not bordered ..... *Oligotrichum*
16. Leaf laminae with teeth on abaxial (back) surface; calyptrae naked or with a few hairs ..... *Oligotrichum*
16. Leaf laminae smooth at back; calyptrae densely hairy 17
17. Plants with capsules 18
17. Plants without capsules 20
18. Capsules (2–)4(–6)-angled ..... *Polytrichum*
18. Capsules cylindric 19
19. Capsules without stomates; lumina of apical cells of lamellae not pyriform ..... *Pogonatum*
19. Capsules with stomates; lumina of apical cells of lamellae pyriform ..... *Polytrichastrum*
20. Apical cells of lamellae smooth or with faint cuticular ridges 21
20. Apical cells of lamellae papillose 22
21. Plants small, less than 6 mm high; leaves never awned ..... *Pogonatum*
21. Plants larger; leaves with or without awns ..... *Polytrichum*
22. Apical cells of lamellae rounded, quadrate or oblate ..... *Pogonatum*
22. Apical cells elliptic-pyriform ..... *Polytrichastrum*
23. Leaves deeply lobed with lobes linear-terete ..... *Takakia*
23. Leaves never lobed, flattened (although sometimes concave with margins inrolled or recurved) 24
24. Leaves without a costa or costa short and double, double, or single with 2–3 lateral spurs 25
24. Leaves with a single costa to at least midleaf 114
25. Although appearing none, costa single and occupying entire leaf area, thus leaf appearing multistratose 26
25. Costa truly none or double; lamina always unistratose 27
26. Leaves ligulate; green cells (chlorocysts) three-sided in section ..... *Octoblepharum*
26. Leaves lanceolate; green cells four-sided in section ..... *Leucobryum*
27. Upper leaf cells papillose or prorulose 28
27. Upper leaf cells smooth (rarely with minute cuticular roughenings) ... 46
28. Leaf apices hyaline 29
28. Leaf apices concolorous 30
29. Leaf cells with a single, unbranched papilla (on each surface); capsules exserted, ribbed; perichaetial leaves entire; restricted to western North America ..... *Pseudobraunia*
29. Leaf cells with 1–2 forked papillae (on each surface); capsules immersed, smooth; perichaetial leaves ciliate; widespread ..... *Hedwigia*

30. Leaf cells pluripapillose 31
30. Leaf cells unipapillose or prorulose 33
31. Papillae arranged in rows over the lumina; leaf cells more than 5:1 ..... *Taxithelium*
31. Papillae randomly arranged over lumina; leaf cells less than 4:1 32
32. Leaves obtuse; stems complanate-foliate ..... *Erpodium*
32. Leaves short-acuminate; stems symmetrically foliate ..... *Braunia*
33. Plants 2–3-pinnate, each year forming a flattened frond, the fronds arranged in a stair-step ascending pattern ..... *Hylocomium*
33. Plants simple or 1-pinnate, not forming ascending fronds 34
34. Leaves plicate 35
34. Leaves not plicate 36
35. Costa double and extending to above midleaf; leaves spreading to squarrose ..... *Rhytidiadelphus*
35. Costa short and double; leaves falcate-secund ..... *Ctenidium*
36. Plants reddish-black, occurring tightly attached to rocks ..... *Andreaea*
36. Plants greenish, occurring on various substrates 37
37. Plants minute, less than 2 mm, acrocarpous ..... *Ephemerum*
37. Plants large, more than 1 cm, pleurocarpous 38
38. Costa strong and double, extending to near leaf apex ..... *Callicostella*
38. Costa short and double, ending below midleaf 39
39. Alar cells numerous, oblate to rounded, strongly differentiated and extending up the margins; restricted to Pacific Northwest ..... *Pterogonium*
39. Alar cells few, mostly quadrate, scarcely extending up the margins; widespread 40
40. Cells at midleaf more than 5:1 41
40. Cells at midleaf less than 5:1 43
41. Apical leaf cells much shorter than those at midleaf ..... *Taxiphyllum*
41. Apical leaf cells scarcely differentiated 42
42. Leaves slenderly acuminate; prorulose at both upper and lower ends of cells ..... *Chryso-hypnum*
42. Leaves acute; prorulose only at upper ends of cells ..... *Leptohymenium*
43. Stem and branch leaves differentiated ..... *Heterocladium*
43. Stem and branch leaves similar 44
44. Leaves broadly ovate, concave, obtuse to obtuse-apiculate ..... *Myurella*
44. Leaves lanceolate to ovate-lanceolate, acute to acuminate 45
45. Leaves acute, serrulate only above; propagula often in leaf axils; northern in distribution ..... *Pterigynandrum*
45. Leaves acuminate, serrulate throughout; propagula absent; eastern U.S. in distribution ..... *Schwetschkeopsis*
46. Leaves ending in a hyaline awn 47
46. Leaves concolorous at apex 48
47. Leaf cells 2:1 or less, oblate-hexagonal throughout; eperistomate ..... *Erpodium*
47. Leaf cells more than 3:1, upper cells shortly rhomboidal, basal cells quadrate; peristomate ..... *Venturiella*
48. Plants aquatic, occurring submerged at least part of the year; leaves keeled or flat ..... *Fontinalis*
48. Plants sometimes in wet habitats but never occurring submerged; leaves various but never keeled 49
49. Plants acrocarpous, usually less than 4 cm 50
49. Plants pleurocarpous, mostly larger 53

50. Plants occurring on rock 51
50. Plants occurring on bare soil 52
51. Plants reddish-black; capsules valvate ..... *Andreaea*
51. Plants greenish-brown; capsules with four peristome teeth .... *Tetrodontium*
52. Protonemata abundant; capsules ovoid, apiculate; calyptrae campanulate-mitrate, deciduous ..... *Ephemerum*
52. Protonemata sparse; capsules globose; calyptrae very small, persistent ..... *Micromitrium*
53. Costa single with one or sometimes two supplementary costae on each side ..... *Antitrichia*
53. Costa double, or if single very short and without supplementary costae 54
54. Costa long and double, extending to or beyond midleaf 55
54. Costa short and double, usually ending just above leaf base 59
55. Stems with numerous paraphyllia 56
55. Stems lacking paraphyllia 57
56. Stem leaves plicate, decurrent ..... *Hylocomiastrum*
56. Stem leaves not plicate or decurrent ..... *Loeskeobryum*
57. Leaf cells thin-walled, lax, abruptly bordered by elongate cells ..... *Cyclodictyon*
57. Leaf cells firm-walled, not or only gradually bordered 58
58. Plants forming mats; leaves falcate-secund at least at branch apices; exostome teeth striate, furrowed ..... *Trachyxiphium*
58. Plants tufted; leaves somewhat contorted when dry but not falcate; exostome teeth papillose, not furrowed ..... *Lepidopilum*
59. Leaves obtuse; plants small, rare, restricted to the mountains of southeastern U.S. 60
59. Leaves acute to acuminate, at least apiculate; plants mostly larger, widespread 61
60. Leaves asymmetric with a basal lobe ..... *Homaliadelphus*
60. Leaves symmetric without lobe ..... *Bryocrumia*
61. Leaf cells lax, hexagonal 62
61. Leaf cells firm- to thick-walled, rounded to linear 63
62. Lateral and dorsal leaves differentiated in areolation; stems pinnately branched ..... *Vesicularia*
62. Lateral and dorsal leaves with similar areolation; stems irregularly branched ..... *Hookeria*
63. Leaves slenderly long-decurrent ..... *Plagiothecium*
63. Leaves not at all decurrent to broadly auriculate 64
64. Plants slender, thread-like; leaves mostly less than 1 mm long 65
64. Plants larger; leaves more than 1 mm long 67
65. Branch leaves more than 0.5 mm long ..... *Homomallium*
65. Branch leaves less than 0.5 mm long 66
66. Costa short and single; leaf cells rounded-elliptic ..... *Pseudoleskeella*
66. Costa none or very short and double; leaf cells rhombic .... *Platydictya*
67. Leaves falcate-secund 68
67. Leaves straight 84
68. Upper leaf cells oblong-rhombic, ca. 3:1 69
68. Leaf cells more or less linear, more than 6:1 70
69. Alar cells numerous, oblate, extending up the margins in many rows ..... *Leucodon*

69. Alar cells few, oblong-quadrate, in 1–2 rows along the insertion ..... *Sematophyllum*
    70. Plants regularly and closely pinnate, feather-like; fronds flat, erect to ascending, oblong-triangular ..... *Ptilium*
    70. Plants irregularly pinnate to unbranched, not feather-like; stems prostrate to loosely ascending 71
71. Mature branches erect and producing abundant and conspicuous propagula in their upper leaf axils ..... *Platygyrium*
71. Branches not producing propagula in leaf axils 72
    72. Branches curved-secund when dry, erect when moist; alar cells small and quadrate ..... *Pylaisiella*
    72. Branches little altered when dry; alar cells various 73
73. Alar cells when differentiated quadrate, sometimes enlarged but not at all inflated 74
73. Alar cells quadrate to oblong, inflated 79
    74. Stems with paraphyllia ..... *Rhytidiopsis*
    74. Stems without paraphyllia 75
75. Plants very large (stem leaves 3.5–5.0 mm), stems ascending to erect; leaves plicate ..... *Rhytidiadelphus*
75. Plants smaller (stem leaves less than 3.5 mm), stems prostrate to ascending; leaves various 76
    76. Alar cells none or very few; pale propagula often clustered in leaf axils ..... *Isopterygiopsis*
    76. Alar cells distinctly differentiated; clustered propagula lacking 77
77. Plants occurring on wet rocks in mountain streams ..... *Hygrohypnum*
77. Plants in various habitats but not as above 78
    78. Costa to ca. ⅓ the leaf length with the two forks not meeting at the base; plants of Alaska and Yukon ..... *Gollania*
    78. Costa mostly shorter, the forks joining at the base; plants widespread ..... *Hypnum*
79. Plants occurring in calcareous fens or marl pools, dark reddish-brown; leaves obtuse ..... *Scorpidium*
79. Plants occurring in other habitats, golden to green; leaves acute to acuminate 80
    80. Plants occurring on wet rocks in mountain streams ..... *Hygrohypnum*
    80. Plants in various habitats but not as above 81
81. Alar cells thick-walled, inflated in several rows; leaf margins strongly serrate ..... *Heterophyllium*
81. Alar cells inflated in 1(–2) rows, or if more, thin-walled; leaf margins entire to serrulate 82
    82. Stems surrounded by enlarged, thin-walled, hyaline cortical cells (hyalodermis); alar cells in large, subdecurrent areas ..... *Hypnum*
    82. Stems surrounded by small, thick-walled, concolorous cells; alar cells in 1(–2) rows 83
83. Plants very shiny; leaves 0.8–1.4 mm long, densely serrulate above; capsules inclined, asymmetric ..... *Brotherella*
83. Plants slightly shiny; leaves 0.5–1.1 mm long, distantly serrulate above; capsule erect, symmetric ..... *Pylaisiadelpha*
    84. Stem leaves abruptly contracted to long setaceous point 85
    84. Stem leaves acute, acuminate or apiculate 86

85. Leaf apices hyaline; alar cells scarcely differentiated ..... *Iwatsukiella*
85. Leaf apices yellow; alar cells inflated and hyaline ..... *Wijkia*
    86. Leaves squarrose-recurved when dry, with channeled apices 87
    86. Leaves erect to spreading, or if squarrose only when moist, the apices mostly not channeled 88
87. Stem leaves greater than 2.5 mm long; alar cells oblong, somewhat inflated, intramarginal ..... *Rhytidiadelphus*
87. Stem leaves less than 2.5 mm long; alar cells subquadrate, not at all inflated, marginal ..... *Campylium*
    88. Plants occurring on wet rocks in mountain streams; leaves ovate, concave ..... *Hygrohypnum*
    88. Plants in other habitats but not as above; leaves various 89
89. Stems complanate-foliate 90
89. Stems symmetrically foliate 96
    90. Alar cells numerous and quadrate; capsules erect ..... *Entodon*
    90. Alar cells few, variously shaped; capsules usually inclined 91
91. Plants occurring on vertical substrates, tree trunks or rocks ..... *Neckera*
91. Plants occurring on horizontal substrates, rarely the extreme bases of trees 92
    92. Leaf margins serrulate throughout 93
    92. Leaf margins entire or serrulate only in upper half 94
93. Apical leaf cells shorter than those at midleaf ..... *Taxiphyllum*
93. Apical leaf cells undifferentiated ..... *Herzogiella*
    94. Rhizoids arising from leaf axils, papillose; leaf margins more or less entire ..... *Isopterygiopsis*
    94. Rhizoids arising from below leaf insertion, smooth; leaf margins serrulate above 95
95. Pseudoparaphyllia filamentous; annuli not differentiated; plants mostly monoicous ..... *Isopterygium*
95. Pseudoparaphyllia absent; annuli differentiated; plants mostly dioicous ..... *Pseudotaxiphyllum*
    96. Alar cells inflated 97
    96. Alar cells rectangular to quadrate, not inflated 101
97. Plants erect; stems with hyalodermis; alar cells hyaline and in auricles ..... *Calliergonella*
97. Plants prostrate; stems without hyalodermis; alar cells yellowish, not in auricles 98
    98. Alar cells uniform, without an enlarged basal row; stem apices flattened ..... *Callicladium*
    98. Alar cells with an enlarged basal row; stem apices not flattened ... 99
99. Alar cells rounded to the insertion; exostome teeth furrowed .. *Acroporium*
99. Alar cells not rounded to insertion; exostome teeth not furrowed 100
    100. Exostome teeth striate; endostome with evident basal membrane and segments; eastern North America ..... *Sematophyllum*
    100. Exostome teeth smooth or faintly papillose; endostome fugaceous, appearing absent; restricted to oak scrub in central Florida ..... *Donnellia*
101. Plants with numerous (more than 50), quadrate alar cells, extending up the margins by more than 12 rows 102
101. Plants with fewer (less than 25), quadrate to rectangular alar cells, extending up the margins in less than 8 rows 107

102. Stems with numerous paraphyllia ..... *Alsia*
102. Stems lacking paraphyllia 103
103. Leaves less than 0.8 mm long; cells with obscure cuticular roughenings; western montane ..... *Leptopterigynandrum*
103. Leaves more than 1 mm long; cells smooth 104
104. Alar cells extending up the margins for less than ⅙ the leaf length 105
104. Alar cells extending up the margins for more than ⅓ the leaf length 106
105. Leaves acuminate, somewhat decurrent; endostome with cilia; plants restricted to coastal western North America, California to British Columbia ..... *Tripterocladium*
105. Leaves mostly obtuse to acute, rarely acuminate, never decurrent; endostome lacking cilia; plants widespread but not in coastal western North America ..... *Entodon*
106. Secondary stems freely subpinnately branched ..... *Forsstroemia*
106. Secondary stems simple or with few branches ..... *Leucodon*
107. Plants epiphytic with creeping primary stems and erect secondary stems 108
107. Plants terrestrial or rarely on bases of trees, primary and secondary stems not differentiated 109
108. Secondary stems unbranched; leaves spreading with squarrose tips; propagula common ..... *Jaegerina*
108. Secondary stems irregularly branched; leaves erect; propagula absent ..... *Neomacounia*
109. Stems with hyalodermis; leaf margins serrulate to base ..... *Herzogiella*
109. Stems without hyalodermis; leaf margins entire or serrulate above ... 110
110. Leaves plicate ..... *Orthothecium*
110. Leaves not plicate 111
111. Leaf apices obtuse-apiculate 112
111. Leaf apices acuminate 113
112. Plants occurring in fens; stems green, sparsely branched ..... *Pseudocalliergon*
112. Plants widespread in acidic habitats of the boreal forest; stems reddish-orange, pinnately branched ..... *Pleurozium*
113. Leaf cells porose throughout; pseudoparaphyllia absent or foliose; plants in boreal, arctic and alpine habitats ..... *Orthothecium*
113. Leaf cells not porose except at insertion; pseudoparaphyllia filamentous; plants of coastal eastern North America inland to the Midwest ..... *Isopterygium*
114. Plants erect, dendroid or frondose from a nonbranched stipe ... 115
114. Plants prostrate to erect, simple to pinnately branched 121
115. Leaves bordered by elongate cells 116
115. Leaves not bordered 117
116. Plants with two kinds of leaves, the larger ones with costa ending well below apex, the smaller ones (amphigastria) with excurrent costa ..... *Hypopterygium*
116. Plants with leaves all of one kind, the costa subpercurrent ..... *Leucolepis*
117. Stems with paraphyllia or filamentous, paraphyllia-like structures 118

117. Stems without paraphyllia 120
118. Plants epiphytic; stems pinnately frondose, curled when dry, spreading when moist ..... *Dendroalsia*
118. Plants terrestrial (rarely on tree bases); stems dendroid, little altered when dry 119
119. Branch leaves long-decurrent, the decurrencies of inflated, hyaline cells; stems with lamellae; stem leaves with entire margins ..... *Pleuroziopsis*
119. Branch leaves cordate to auriculate, the auricles not inflated; stems with paraphyllia; stem leaves with serrate margins ..... *Climacium*
120. Apical cells of branch leaves rhombic; costa of branch leaves strong, not tapering toward apex ..... *Thamnobryum*
120. Apical cells of branch leaves long-hexagonal; costa of branch leaves slender, tapering toward apex ..... *Porotrichum*
121. Plants blackish, tightly attached to rocks in arctic and montane areas; capsules valvate 122
121. Plants greenish to blackish, on various substrates; capsules cleistocarpous or operculate, never valvate 123
122. Plants occurring on calcareous rocks; capsules not hygroscopic, turbinate, obtuse-conic ..... *Andreaeobryum*
122. Plants occurring on acidic rocks; capsules hygroscopic, when moist elliptic, tapering to a point ..... *Andreaea*
123. Leaves strongly squarrose-recurved wet or dry; plants occurring in fens ..... *Paludella*
123. Leaves erect to squarrose; plants occurring in various habitats 124
124. Stems with paraphyllia 125
124. Stems lacking paraphyllia 142
125. Stems complanate-foliate; stem leaves undulate ..... *Metaneckera*
125. Stems symmetrically foliate; leaves not undulate 126
126. Alar cells inflated in well marked groups 127
126. Alar cells mostly not differentiated, if so, not inflated 128
127. Stem leaves deeply plicate; paraphyllia filamentous, abundant ..... *Palustriella*
127. Stem leaves not plicate; paraphyllia foliose, sparse to abundant ..... *Cratoneuron*
128. Paraphyllia with short cells, 1–3:1 129
128. Paraphyllia with elongate cells, more than 5:1 140
129. Cells of paraphyllia papillose 130
129. Cells of paraphyllia smooth 134
130. Leaf cells unipapillose 131
130. Leaf cells pluripapillose 132
131. Plants once-pinnate; leaf cells papillose on both surfaces ..... *Abietinella*
131. Plants 2–3-pinnate; leaf cells papillose only at back ..... *Thuidium*
132. Plants large, dioicous; leaf cells papillose only at back ..... *Thuidium*
132. Plants small, autoicous; leaf cells papillose on both surfaces 133
133. Plants once-pinnate; leaves not incurved when dry; leaf cells strongly bulging; setae smooth ..... *Rauiella*
133. Plants 1–2-pinnate; leaves incurved when dry; leaf cells flat; setae smooth or papillose ..... *Cyrto-hypnum*
134. Papillae of leaf cells large, either forked or elongate and curved; leaves broadly ovate ..... *Thelia*

134. Papillae of leaf cells small, simple; leaves lanceolate to ovate-lanceolate 135
135. Costa pellucid; leaves usually with hair-points ..... *Claopodium*
135. Costa opaque; leaves lacking hair-points 136
136. Stem and branch leaves differentiated ..... *Haplocladium*
136. Stem and branch leaves uniform 137
137. Leaf cells isodiametric or nearly so, hexagonal to short-rhombic 138
137. Leaf cells elongate, oblong-rhombic to oblong-linear 139
138. Capsules inclined, asymmetric; exostome teeth striate; plants largely western ..... *Pseudoleskea*
138. Capsules erect, symmetric; exostome teeth pale and papillose; plants largely eastern ..... *Leskea*
139. Capsules erect, symmetric; endostome segments narrow, not keeled ..... *Lescuraea*
139. Capsules inclined, asymmetric; endostome segments broader, keeled ..... *Pseudoleskea*
140. Leaf margins entire to serrulate ..... *Helodium*
140. Leaf margins strongly serrate in upper half 141
141. Upper leaf cells short, 2–5:1; plants of southeastern United States ..... *Climacium*
141. Upper leaf cells linear, more than 8:1; plants widespread ..... *Hylocomiastrum*
142. Plants whitish; leaves composed mostly of costa, multistratose, with small green cells enclosed between 2 layers of hyaline cells on both surfaces 143
142. Plants greenish to blackish, rarely whitish; leaves usually with conspicuous lamina, if not green cells and hyaline cells of about equal size with only a single layer of hyaline cells on either side of the green cells 144
143. Green cells in section 4-sided; plants terrestrial ..... *Leucobryum*
143. Green cells in section 3-sided; plants epiphytic ..... *Octoblepharum*
144. Leaf margins strongly incurved to involute, at least when dry 145
144. Leaf margins plane to recurved 149
145. Leaf margins incurved wet or dry 146
145. Leaf margins incurved when dry, plane when moist 148
146. Leaf cells papillose; costa with two stereid bands 147
146. Leaf cells smooth; costa with one stereid band ..... *Indusiella*
147. Capsules exserted, operculate ..... *Weissia*
147. Capsules immersed to emergent, cleistocarpous ..... *Astomum*
148. Costa with single stereid band; peristome present ..... *Neohyophila*
148. Costa with two stereid bands; peristome absent ..... *Hyophila*
149. Plants minute, occurring on soil (or rarely rock), ephemeral, often with persistent protonemata; capsules immersed 150
149. Plants mostly larger, occurring on various substrates, mostly not ephemeral, or if so, capsules exserted 161
150. Capsules operculate 151
150. Capsules cleistocarpous 152
151. Exothecial cells collenchymatous ..... *Aphanorrhegma*
151. Exothecial cells not thickened at corners ..... *Physcomitrium*
152. Spores few per capsule, more than 100 μm in diameter 153

152. Spores numerous per capsule, less than 60 μm in diameter 154
153. Leaves broadly ovate or elliptic, abruptly narrowed to an awn; plants with slender, subterranean rhizomes ..... *Lorentziella*
153. Leaves oblong to lanceolate, acute to subulate; plants not rhizomatous ..... *Archidium*
154. Leaves ovate to broadly ovate, abruptly cuspidate to apiculate .. 155
154. Leaves narrowly lanceolate to oblong; costa subpercurrent to subulate 157
155. Leaf cells pluripapillose with C-shaped papillae; leaf margins revolute ..... *Phascum*
155. Leaf cells smooth or with 1–2 blunt, conical papillae; leaf margins plane to erect 156
156. Plants bulbiform, occurring on soil; leaves very broad and deeply concave with a reflexed tip ..... *Acaulon*
156. Plants not bulbiform, occurring on the underside of quartz pebbles; leaves oblong-lanceolate to oblong-ovate, the tip not reflexed ..... *Aschisma*
157. Capsules pyriform with a conspicuous stomatose neck ..... *Bruchia*
157. Capsules globose to broadly elliptic without a conspicuously differentiated neck 158
158. Costa long excurrent, at least on perichaetial leaves ..... *Pleuridium*
158. Costa subpercurrent 159
159. Leaf margins spinose-serrulate throughout ..... *Ephemerum*
159. Leaf margins entire or serrulate above 160
160. Leaves lanceolate ..... *Pseudephemerum*
160. Leaves oblong-lanceolate to obovate ..... *Physcomitrella*
161. Neck of capsules (apophysis) as wide or wider than upper portion (urn); occurring on dung and animal remains 162
161. Neck of capsules considerably narrower than urn; occurring on various substrates 164
162. Capsules dumb-bell shaped when mature; seta hyaline; restricted to the arctic ..... *Aplodon*
162. Capsules (at least the urn) cylindric; seta colored; widespread .. 163
163. Apophyses narrowly pyriform, the same color or darker than the urn; peristome teeth joined in 4's, later in 2's, not chambered ..... *Tetraplodon*
163. Apophyses globose to turbinate, sometimes becoming umbrella-like, differentiated in color; peristome teeth sometimes approximate or fused in pairs, chambered ..... *Splachnum*
164. Leaves of two kinds, large lateral ones and smaller dorsal ones . 165
164. Leaves all of one kind 166
165. Leaves bordered; plants erect, occurring along the Pacific coast ..... *Epipterygium*
165. Leaves unbordered; plants prostrate, restricted to southern Florida ..... *Racopilum*
166. Capsules cleistocarpous; plants rare 167
166. Capsules operculate; plants rare to common 169
167. Plants known only from New Hampshire; occurring on wet soil ... *Bruchia*
167. Plants known from arctic and alpine tundra on animal-derived substrates 168
168. Capsules broadest in lower half ..... *Voitia*

168. Capsules broadest in upper half ..... *Tetraplodon*
169. Cells with nodulose-wavy walls throughout the leaf, sometimes most conspicuous toward leaf base when upper cells short ..... *Racomitrium*
169. Cells without nodulose-wavy walls, or if present only near insertion .. 170
170. Leaves with hyaline hair-points 171
170. Leaves without hair-points, or if with hair-points not hyaline ... 181
171. Costa broad, filling ¼ or more of the leaf base ..... *Campylopus*
171. Costa narrower 172
172. Upper leaf cells densely pluripapillose with C-shaped papillae .. 173
172. Upper leaf cells smooth or with low, indistinct papillae 174
173. End walls of basal cells thickened; calyptrae large, mitrate and covering capsule ..... *Encalypta*
173. End walls of basal cells not thickened; calyptrae small, cucullate ... *Tortula*
174. Cells smooth, lax, thin-walled, hexagonal to rhombic 175
174. Cells obscurely papillose, firm-walled, rounded to quadrate 177
175. Leaves not bordered ..... *Stegonia*
175. Leaves bordered 176
176. Plants usually epiphytic; capsules erect ..... *Brachymenium*
176. Plants terrestrial or saxicolous; capsules inclined ..... *Bryum*
177. Plants occurring on trees ..... *Orthotrichum*
177. Plants occurring on rocks and soil 178
178. Perichaetial leaves differentiated in size and shape; capsules immersed ..... *Schistidium*
178. Perichaetial leaves similar to upper vegetative leaves; capsule immersed or exserted 179
179. Calyptrae scarcely longer than the operculum, cucullate or mitrate, smooth ..... *Grimmia*
179. Calyptrae large, covering the capsule to the middle or below, campanulate-mitrate, striate or plicate 180
180. Leaves lanceolate; annuli none; calyptrae plicate ..... *Coscinodon*
180. Leaves ovate to obovate; annuli well developed; calyptrae striate ..... *Jaffueliobryum*
181. Costa very broad, occupying ⅓–½ the leaf base and filling the subula (plants entirely acrocarpous) 182
181. Costa narrower, or if broad then ending below the leaf apex and not filling it (or if broad then pleurocarpous) 187
182. Alar cells well differentiated 183
182. Alar cells poorly differentiated 185
183. Costa without guide cells or stereids, in transverse section with a median layer of green cells enclosed dorsally and ventrally with hyaline cells ..... *Paraleucobryum*
183. Costa nearly always with guide cells and stereids, without enclosed green cells 184
184. Inner basal cells of leaf pale, enlarged, and broadly rectangular, extending upward along the costa; capsules smooth; annuli none; calyptrae not fringed ..... *Dicranodontium*
184. Inner basal cells not conspicuously differentiated along the costa; capsules furrowed; annuli compound; calyptrae usually fringed ..... *Campylopus*
185. Capsules with a neck at least as long as the urn; costa filling no more than ⅓ of the leaf base ..... *Trematodon*

185. Capsules with a short, inconspicuous neck; costa filling ½ or more of the leaf base 186
186. Leaves 3.5–5.0 mm long; upper laminal cells elongate, 75–140 μm long; brood leaves absent ..... *Campylopodiella*
186. Leaves 2.0–3.0 mm long; upper laminal cells rectangular, 25–55 μm long; brood leaves usually present, often abundant ..... *Brothera*
187. Plants pleurocarpous (sporophytes lateral); stems mostly prostrate with lateral branches, often mat-forming, or stems prostrate with erect branches bearing terminal sporophytes (cladocarpous) 188
187. Plants acrocarpous (sporophytes terminal); stems erect, not branched or occasionally branched beneath inflorescences 280
188. Leaves bordered by elongate cells, sharply differentiated from shorter inner cells 189
188. Leaves not bordered by elongate cells 191
189. Plants epiphytic; border unistratose ..... *Daltonia*
189. Plants aquatic; border 2–5-stratose 190
190. Margins serrate almost to base; leaves ovate-oblong to ovate-lanceolate, acuminate; plants of Oregon ..... *Limbella*
190. Margins serrulate; leaves ovate, often broadly so, bluntly acute; plants of eastern North America ..... *Platylomella*
191. Leaf cells papillose or prorulose 192
191. Leaf cells smooth 205
192. Leaves rugose and plicate ..... *Rhytidium*
192. Leaves not rugose, rarely plicate 193
193. Leaf cells pluripapillose 194
193. Leaf cells unipapillose or prorulose 198
194. Papillae arranged in a row over the cell lumina; cells longer than 3:1 195
194. Papillae randomly arranged over the cells; cells more or less isodiametric 196
195. Plants stiff, dark green to blackish; leaves ovate, plicate, cordate ..... *Papillaria*
195. Plants soft, bright green (when alive); leaves lanceolate, smooth, not cordate ..... *Barbella*
196. Leaf apices fragile ..... *Haplohymenium*
196. Leaf apices not fragile 197
197. Leaves strongly inrolled when dry; marginal basal cells elongate, smooth; sporophytes terminal on branches ..... *Macromitrium*
197. Leaves loosely erect to contorted; marginal basal cells rounded, papillose; sporophytes lateral ..... *Anomodon*
198. Cells unipapillose over the lumina 199
198. Cells prorulose 201
199. Upper leaf cells linear-flexuose; uniseriate propagula common in leaf axils ..... *Henicodium*
199. Upper leaf cells short, 1–3:1; asexual reproduction absent or by branchlets 200
200. Leaves ovate-lanceolate, narrowed to a nonpapillose, pale acumen, squarrose when moist ..... *Lindbergia*
200. Leaves oblong-ovate, bluntly acute, loosely erect and more or less complanate ..... *Stereophyllum*
201. Leaf cells short, 1–3:1 202

201. Leaf cells more than 5:1 203
202. Leaves appressed when dry, wide-spreading when moist; perichaetial leaves strongly differentiated; capsules immersed ..... *Cryphaea*
202. Leaves little altered when moist; perichaetial leaves scarcely differentiated; capsules exserted ..... *Lescuraea*
203. Plants epiphytic with inconspicuous, creeping, primary stem and erect secondary stems; costa subpercurrent ..... *Pireella*
203. Plants terrestrial and epiphytic, with primary and secondary stems not differentiated; costa ending well below the apex 204
204. Leaves decurrent; setae rough; capsules inclined; plants largely terrestrial ..... *Bryhnia*
204. Leaves not decurrent; setae smooth; capsules erect; plants epiphytic or saxicolous ..... *Isothecium*
205. Leaf apices rounded-obtuse to truncate 206
205. Leaf apices acuminate to bluntly acute 212
206. Leaf apices truncate ..... *Neckeropsis*
206. Leaf apices rounded-obtuse 207
207. Upper leaf cells less than 3:1 208
207. Upper leaf cells (not apical ones) more than 5:1 209
208. Plants strongly complanate, shiny, little altered when moist ..... *Homalia*
208. Plants at best weakly complanate, dull, strongly incurved when dry, erect when moist ..... *Leptodon*
209. Alar cells inflated 210
209. Alar cells not at all inflated 211
210. Plants strongly julaceous; leaves concave; occurring in or near streams ..... *Scleropodium*
210. Plants with loosely spreading leaves; leaves only slightly concave; occurring in fens ..... *Calliergon*
211. Costa ending in a spine ..... *Platyhypnidium*
211. Costa not projecting at apex ..... *Hygrohypnum*
212. Upper leaf cells 1–2:1 213
212. Upper leaf cells more than 5:1 227
213. Sporophytes terminal on erect branches; upper cells rounded 214
213. Sporophytes lateral; upper cells rhombic to subquadrate 217
214. Basal marginal cells short, rounded-quadrate 215
214. Basal marginal cells elongate 216
215. Upper leaf cells strongly bulging; leaves lanceolate; calyptrae hairy, mitrate ..... *Macrocoma*
215. Upper leaf cells flat; leaves oblong-lanceolate; calyptrae naked, cucullate ..... *Drummondia*
216. Inner basal leaf cells subquadrate to rounded; calyptrae short, plicate ..... *Groutiella*
216. Inner basal cells linear; calyptrae long, not plicate ..... *Schlotheimia*
217. Costa strongly flexuose above; leaf margins with multicellular teeth ..... *Herpetineuron*
217. Costa straight or faintly flexuose; leaf margins entire to serrulate 218
218. Costa ending in the leaf apex 219
218. Costa ending well below the leaf apex 223

219. Upper leaf cells thick-walled, rounded-quadrate to elliptic 220
219. Upper leaf cells firm-walled, short-oblong to rhombic 222
220. Plants with clusters of axillary brood branchlets ..... *Leskeella*
220. Plants without brood branchlets 221
221. Alar cells extending to the costa; inner basal cells not differentiated; peristome white ..... *Lindbergia*
221. Alar cells restricted in 5–6 rows along the margins, not reaching the costa; inner basal cells long rectangular; peristome yellow ..... *Pseudoleskeella*
222. Costa relatively narrow, less than 35 μm wide at base; plants terrestrial ..... *Amblystegium*
222. Costa relatively broad, mostly more than 50 μm at base; plants aquatic ..... *Hygroamblystegium*
223. Plants with secondary stems erect and branched 224
223. Plants without differentiated secondary stems, prostrate 225
224. Leaf apices shortly acuminate; leaves more than 1 mm long; plants eastern ..... *Forsstroemia*
224. Leaf apices broadly acute; leaves less than 1 mm long; plants western ..... *Porotrichum (Bryolawtonia)*
225. Leaves acuminate, often homomallous ..... *Pseudoleskeella*
225. Leaves bluntly acute 226
226. Leaves obliquely asymmetric at tip; exostome teeth cross-striate; plants boreal and arctic ..... *Myrinia*
226. Leaves symmetric; exostome teeth rudimentary; plants of southeastern North America ..... *Clasmatodon*
227. Plants bearing long, deciduous, flagelliform branches .... *Pseudocryphaea*
227. Plants without flagelliform branches 228
228. Plants with inconspicuous, creeping primary stems with reduced leaves and erect, leafy secondary stems 229
228. Plants without differentiated stems 232
229. Secondary stems mostly unbranched ..... *Jaegerina*
229. Secondary stems irregulary pinnate 230
230. Costa toothed at back on secondary stem leaves; branch leaves acute ..... *Bestia*
230. Costa smooth at back; branch leaves acuminate 231
231. Leaf margins revolute nearly throughout, serrate above, often with reflexed teeth; costa often with supplementary costae; western in distribution (disjunct in Newfoundland) ..... *Antitrichia*
231. Leaf margins reflexed, entire to serrulate; costa without supplementary costae; eastern in distribution ..... *Forsstroemia*
232. Plants aquatic, coarse; costa broad, more than 100 μm wide at base, bluntly excurrent 233
232. Plants of various habitats; costa much narrower, ending below the apex to excurrent, if excurrent then finely so 234
233. Costa about ⅓ the width of the leaf base; the lamina with multistratose streaks ..... *Donrichardsia*
233. Costa about ¼ the width of the leaf base; the lamina unistratose throughout ..... *Hygroamblystegium*
234. One side of stems for entire length covered by reddish rhizoidal tomentum; leaves strongly plicate ..... *Tomentypnum*

234. Tomentum, if present, restricted to extreme base of stems; leaves plicate or not 235
235. Leaves falcate-secund 236
235. Leaves straight 248
236. Stems with a hyalodermis 237
236. Stems without a hyalodermis 239
237. Leaves strongly plicate, distinctly denticulate in upper portion ... *Sanionia*
237. Leaves striolate to plane, entire to slightly denticulate 238
238. Alar cells inflated; plants occurring in streams ..... *Hygrohypnum*
238. Alar cells poorly differentiated; plants occurring in rich fens ..... *Limprichtia*
239. Plants of upland habitats; leaves plicate ..... *Brachythecium*
239. Plants of wet habitats; leaves not plicate 240
240. Leaves keeled, distinctly to obscurely 3-ranked; endostome segments joined at tips ..... *Dichelyma*
240. Leaves not keeled or 3-ranked; endostome segments free 241
241. Costa excurrent 242
241. Costa subpercurrent 244
242. Alar cells poorly differentiated ..... *Drepanocladus*
242. Alar cells abruptly inflated 243
243. Leaf margins entire ..... *Drepanocladus*
243. Leaf margins finely denticulate ..... *Warnstorfia*
244. Leaf margins finely denticulate at apex ..... *Warnstorfia*
244. Leaf margins entire throughout 245
245. Plants on rocks in mountain streams ..... *Hygrohypnum*
245. Plants in fens and seeps, not on rocks 246
246. Cells in lower half of leaf porose; plants of the arctic ... *Loeskypnum*
246. Cells not porose except at extreme insertion; plants widespread 247
247. Stems with central strand ..... *Drepanocladus*
247. Stems without central strand ..... *Hamatocaulis*
248. Leaves 3-ranked, conduplicate ..... *Brachelyma*
248. Leaves not 3-ranked or conduplicate 249
249. Plants pendulous from branches; stem leaves with capillary points; branch leaves recurved; plants restricted to southernmost Florida ..... *Zelometeorium*
249. Plants terrestrial to epiphytic, never pendulous; stem leaves with shorter points; branch leaves mostly not squarrose; plants mostly more northern 250
250. Leaf cells long-hexagonal, less than 8:1 251
250. Leaf cells linear, more than 10:1 258
251. Leaves broadly ovate, deeply concave; restricted to Alaska ... *Myuroclada*
251. Leaves lanceolate to ovate, not or only slightly concave; widespread 252
252. Plants epiphytic 253
252. Plants terrestrial and saxicolous 254
253. Leaf margins entire; leaf apex gradually acuminate; peristome double and reflexed ..... *Anacamptodon*
253. Leaf margins mostly toothed; leaf apex piliferous; peristome single to absent ..... *Fabronia*

254. Leaf apices piliferous ..... *Fabronia*
254. Leaf apices acute to acuminate 255
255. Upper leaf cells thick-walled, with rounded ends; capsules erect ..... *Pseudoleskeella*
255. Upper leaf cells firm-walled, with pointed ends; capsules inclined 256
256. Plants on soil in dry habitats, especially prairies ..... *Brachythecium*
256. Plants on logs and soil in mesic to wet habitats 257
257. Leaves greater than 1 mm long ..... *Leptodictyum*
257. Leaves less than 1 mm long ..... *Amblystegium*
258. Plants attached to rocks in fast-flowing streams and beside waterfalls ..... *Platyhypnidium*
258. Plants in various habitats but not on rocks in fast-flowing water . 259
259. Plants terrestrial, large, coarse, erect; stems pinnately branched 260
259. Plants various, prostrate to ascending, if erect then in wetlands; branching various 261
260. Stem leaves ovate-lanceolate, acuminate to filiform, plicate; plants on litter in coniferous forests ..... *Trachybryum*
260. Stem leaves ovate-oblong, abruptly apiculate, not plicate; plants in lawns and gardens ..... *Pseudoscleropodium*
261. Leaves plicate 262
261. Leaves not plicate 264
262. Branches curved-ascending when dry ..... *Homalothecium*
262. Branches prostrate 263
263. Leaf apices coarsely serrate; upper leaf cells thick-walled; alar cells well differentiated, quadrate; plants rigid ..... *Palamocladium*
263. Leaf apices entire to serrulate; upper leaf cells firm-walled; alar cells mostly differentiated, short-rectangular; plants soft ..... *Brachythecium*
264. Plants on tree trunks; calyptrae sparsely hairy; setae rough; plants of eastern U.S. ..... *Homalotheciella*
264. Plants not on tree trunks except rarely at bases, if on trees plants of western North America; calyptrae naked; setae usually smooth, rarely rough 265
265. Plants terete, at least at apex; leaves broadly oblong to ovate, concave to cucullate 266
265. Plants with spreading leaves; leaves lanceolate, not or scarcely concave 272
266. Leaves abruptly acuminate 267
266. Leaves broadly acute to obtuse, sometimes with a minute apiculus 269
267. Costa with one or more spines at the tip; plants of western North America ..... *Scleropodium*
267. Costa without spines at tip; plants widespread 268
268. Leaf apex filiform, flat ..... *Cirriphyllum*
268. Leaf apex broader, twisted ..... *Bryoandersonia*
269. Leaves with minute apiculus 270
269. Leaves not apiculate 271
270. Plants green; basal leaf cells porose ..... *Loeskypnum*
270. Plants reddish; basal leaf cells not porose ..... *Sarmenthypnum*
271. Leaves obtuse; plants occurring in fens and swamps; widespread ..... *Calliergon*

271. Leaves broadly acute; plants occurring on moist rocks and soil; Pacific coast ..... *Scleropodium*
    272. Branch leaves with apical cells about ½ the length of those at midleaf ..... *Eurhynchium*
    272. Branch leaves with apical cells scarcely shorter than those at midleaf 273
273. Leaf apices twisted; stems often complanate-foliate ..... *Steerecleus*
273. Leaf apices flat; stems rarely complanate-foliate 274
    274. Leaves with channeled leaf apices from a concave base, with a narrow insertion ..... *Campylium*
    274. Leaves without channeled leaf apices, the leaf base not concave or with a narrow insertion 275
275. Alar cells numerous and quadrate with more on one side of the costa than the other, collenchymatous; plants of southernmost Florida ..... *Entodontopsis*
275. Alar cells few, symmetrically arranged, not collenchymatous; plants widespread 276
    276. Branch and stem leaves strongly differentiated; opercula long rostrate ..... *Eurhynchium*
    276. Branch and stem leaves scarcely differentiated; opercula conic to apiculate 277
277. Costa percurrent or nearly so 278
277. Costa ending well below leaf apex 279
    278. Costa indistinct at midleaf, not toothed; setae smooth; propagula uniseriate, often formed on back of costa at apex ..... *Conardia*
    278. Costa distinct throughout, toothed at back above; setae rough; propagula not present ..... *Brachythecium*
279. Leaves wide-spreading with entire margins; stems complanate-foliate; plants occurring in wet habitats ..... *Leptodictyum*
279. Leaves erect to spreading with serrulate margins, rarely entire; stems not complanate-foliate; plants occurring in various habitats .... *Brachythecium*
    280. Capsules large, sessile, asymmetric ..... *Diphyscium*
    280. Capsules smaller, usually exserted, symmetric 281
281. Costa ridged at back 282
281. Costa smooth or toothed at back, not ridged 283
    282. Leaf cells rounded-oblate ..... *Dryptodon*
    282. Leaf cells long-rectangular, more than 5:1 ..... *Dicranum*
283. Conspicuous clusters of dark rhizoids obscuring the stem 284
283. Rhizoids inconspicuous or if obvious, never obscuring the stem 287
    284. Leaf cells strongly unipapillose on both surfaces ..... *Aulacomnium*
    284. Leaf cells smooth or prorulose 285
285. Leaves narrowly lanceolate from an ovate base ..... *Anacolia*
285. Leaves ovate to broadly elliptic 286
    286. Rhizoidal (macronematal) initials in longitudinal rows; endostome fused into a dome ..... *Cinclidium*
    286. Rhizoidal initials not in longitudinal rows; endostome segments free ..... *Rhizomnium*
287. Plants blackish, occurring on wet rocks usually near streams or the sea, never with propagula 288
287. Plants greenish, occurring in various habitats, rarely on wet rocks by streams, with or without propagula 290

288. Leaf bases with submarginal band of elongate cells ..... *Scouleria*
288. Leaf bases without differentiated submarginal cells 289
289. Leaf margins incurved ..... *Grimmia*
289. Leaf margins plane to recurved ..... *Schistidium*
290. Hyaline basal cells extending up the margins farther than at the costa, forming a V-shaped area 291
290. Hyaline basal cells if present extending more or less equally up the margins as costa or farther up the costa 293
291. Upper cells bulging but not papillose ..... *Luisierella*
291. Upper cells pluripapillose 292
292. Leaves squarrose-recurved from an erect base when moist; leaf margins serrulate above; sporophytes lateral ..... *Pleurochaete*
292. Leaves erect-spreading to spreading from an erect base when moist; leaf margins entire to notched; sporophytes terminal ..... *Tortella*
293. Plants glaucous, bluish-green ..... *Saelania*
293. Plants not glaucous or bluish 294
294. Leaves bordered by 2 or more rows of elongate cells 295
294. Leaves unbordered or if bordered then by only a single row of somewhat elongate cells, or by short cells 309
295. Leaf margins entire 296
295. Leaf margins toothed, sometimes obscurely so 300
296. Leaf cells longer than 3:1 297
296. Leaf cells 1–2:1 298
297. Leaf cells in oblique rows; leaves rounded-obtuse, bluntly apiculate ..... *Pseudobryum*
297. Leaf cells not in obvious rows; leaves various ..... *Bryum*
298. Rhizoidal (macronematal) initials in longitudinal rows; endostome fused to a dome ..... *Cinclidium*
298. Rhizoidal initials not in longitudinal rows; endostome segments free 299
299. Leaves bluntly acute; border unistratose; stems blackish; stomates superficial ..... *Cyrtomnium*
299. Leaves emarginate, rounded-apiculate; border various; stems reddish; stomates immersed ..... *Rhizomnium*
300. Leaves lanceolate from an expanded base, the base with numerous, abruptly hyaline cells ..... *Syrrhopodon*
300. Leaves without expanded base, without hyaline cells 301
301. Leaf margins with paired teeth 302
301. Leaf margins with single teeth 304
302. Leaf cells strongly bulging ..... *Trachycystis*
302. Leaf cells flat 303
303. Some leaves with low, inconspicuous lamellae; costa in transverse section with two stereid bands; peristome of 32 small teeth attached at tips to a tympanum ..... *Atrichum*
303. No leaves with lamellae; costa with or without a single stereid band; exostome of 16 free teeth ..... *Mnium*
304. Leaves rugose wet or dry; plants restricted to Pacific Northwest ..... *Roellia*
304. Leaves flat when wet, contorted but not rugose when dry; plants widespread 305
305. Leaf cells shorter than 2:1 ..... *Plagiomnium*

305. Leaf cells 3:1 or more 306
306. Stems rosulate-foliate, occurring erect from a horizontal underground stem; sporophytes often clustered ..... *Rhodobryum*
306. Stems foliate throughout, without rhizome-like connections between erect stems; sporophytes not clustered 307
307. Leaf cells in oblique rows; leaves rounded-obtuse, apiculate ..... *Pseudobryum*
307. Leaf cells not in obvious rows; leaves broadly acute to acuminate 308
308. Capsules erect and symmetric; endostome with a high basal membrane, segments lacking or rudimentary, cilia absent ..... *Brachymenium*
308. Capsules inclined and asymmetric; endostome with a keeled basal membrane, keeled and perforate segments, and usually with cilia ..... *Bryum*
309. Leaf margins with paired teeth 310
309. Leaf margins with single teeth or entire 315
310. Leaf bases with abruptly differentiated colorless cells (cancellinae); propagula borne on costa near apex ..... *Syrrhopodon*
310. Leaf bases without cancellinae; propagula absent 311
311. Leaf cells smooth 312
311. Leaf cells prorulose or with fine cuticular ridges 313
312. Leaves elliptic to ovate-elliptic ..... *Mnium*
312. Leaves linear-lanceolate ..... *Pyrrhobryum*
313. Upper leaf cells with cuticular ridges; stems triangular in transverse section ..... *Plagiopus*
313. Upper leaf cells prorulose; stems round in transverse section 314
314. Leaves crispate when dry ..... *Bartramia*
314. Leaves straight when dry ..... *Philonotis*
315. Leaf cells strongly bulging on one or both surfaces, not papillose 316
315. Leaf cells flat, smooth or papillose, or if bulging then papillose 318
316. Leaf laminae bistratose ..... *Timmiella*
316. Leaf laminae unistratose 317
317. Plants with sheathing leaf bases ..... *Timmia*
317. Plants without sheathing leaf bases ..... *Bryobrittonia*
318. Leaves with abruptly expanded, sheathing leaf bases 319
318. Leaves with leaf bases not or only gradually expanded, rarely sheathing 326
319. Leaf cells papillose (at least on sheath) or prorulose 320
319. Leaf cells smooth 321
320. Leaf cells papillose over the lumina ..... *Timmia*
320. Leaf cells prorulose ..... *Bartramia*
321. Upper leaf cells quadrate 322
321. Upper leaf cells short-rectangular 323
322. Capsules inclined and asymmetric, strumose; plants widespread ..... *Oncophorus*
322. Capsules erect, symmetric, not strumose; plants restricted to southwestern U.S. ..... *Symblepharis*
323. Awns roughened throughout by projecting cell ends ..... *Trichodon*
323. Awns smooth or only rough at apex 324
324. Capsules with neck as long as or longer than the urn ..... *Trematodon*
324. Capsules with neck much shorter than the urn 325

325. Capsules erect, cylindric, smooth; peristome teeth irregularly perforate or deeply cleft into terete, sometimes filiform divisions ..... *Ditrichum*
325. Capsules inclined, oblong, smooth or furrowed, if erect then furrowed; peristome teeth flat, split ½ way down, vertically pitted ..... *Dicranella*
326. Alar cells enlarged, colored, or inflated 327
326. Alar cells scarcely differentiated 333
327. Upper and median leaf cells with coarse, irregular cuticular ridges, resembling papillae in transverse section; capsules cylindric, smooth, erect 328
327. Leaf cells without cuticular ridges; capsules various 329
328. Leaves with clusters of spherical propagula at leaf apex; leaf margins bistratose ..... *Grimmia*
328. Leaves without propagula; leaf margins unistratose .... *Dicranoweisia*
329. Costa with 2 stereid bands ..... *Dicranum*
329. Costa without stereids 330
330. Capsules curved, strumose; plants on alpine rocks ..... *Kiaeria*
330. Capsules erect, not strumose; plants widespread 331
331. Capsules cylindric; plants usually terrestrial or on tree trunks, rarely on rock ..... *Dicranum*
331. Capsules short, obovoid to pyriform; plants on rocks 332
332. Capsules ribbed when dry; peristome vertically pitted-striolate below ..... *Arctoa*
332. Capsules smooth when dry; peristome papillose ..... *Blindia*
333. Leaf cells smooth 334
333. Leaf cells papillose or prorulose 398
334. Asexual propagula borne on the leaf surfaces ..... *Rhachithecium*
334. Asexual propagula absent, axillary or on leaf apices or specialized structures 335
335. Leaves ovate to obovate, broadly obtuse, with the costa ending below the leaf apex 336
335. Leaves linear, ovate-lanceolate, ligulate to ovate, acuminate to acute or awned, with costa ending below the apex to excurrent 342
336. Leaf apices cucullate ..... *Globulinella*
336. Leaf apices not cucullate 337
337. Plants with large, multicellular propagula in leaf axils; leaves obovate, with cilia on the basal margins ..... *Oedipodium*
337. Plants without axillary propagula; leaves ovate to spatulate, eciliate .. 338
338. Plants small and bulbiform, on dry soil; leaves concave and imbricate ..... *Stegonia*
338. Plants small to medium-sized, never bulbiform, on moist soil; leaves flat to concave, mostly not imbricate 339
339. Leaf cells short-rectangular, lax, thin-walled; capsules erect 340
339. Leaf cells long-hexagonal, firm-walled; capsules inclined to horizontal 341
340. Apical marginal leaf cells short-rhombic, oblong-hexagonal internally; capsules without a distinct neck; plants of southern United States ..... *Splachnobryum*
340. Apical marginal leaf cells laxly rectangular, similar to internal ones; capsules with well differentiated neck; plants northern ..... *Tayloria*
341. Plants whitish-green, terete; upper leaf cells long, 7–9:1 .... *Anomobryum*
341. Plants reddish or green, not terete; upper cells shorter, 2–6:1 ..... *Bryum*

342. Leaves oblong, lingulate to ovate 343
342. Leaves lanceolate to linear 368
343. Leaf cells rounded to quadrate, more or less isodiametric 344
343. Leaf cells short-rectangular to linear 353
344. Leaf bases with abruptly differentiated, hyaline cells (cancellinae); leaf apices often with propagula ..... *Calymperes*
344. Leaf bases without cancellinae although sometimes gradually hyaline; leaf apices without propagula 345
345. Costa excurrent to ending in the cusp; leaf apex cuspidate to piliferous 346
345. Costa subpercurrent; leaf apex broadly acute or obtuse to rarely mucronate 349
346. Leaf apices piliferous ..... *Desmatodon*
346. Leaf apices cuspidate 347
347. Plants with rhizoidal tubers, known only from Louisiana; capsules unknown ..... *Tortula (Chenia)*
347. Plants lacking tubers, widespread in the north; capsules exserted 348
348. Capsules 0.4–0.8 mm long, obovoid; spores more than 20 μm in diameter; peristome absent or rudimentary; plants boreal-temperate ..... *Pottia*
348. Capsules 2.5–3.5 mm long, cylindric; spores less than 20 μm in diameter; peristome well developed with twisted teeth from a basal membrane; plants of tundra ..... *Crumia*
349. Peristome teeth four; propagula cups borne on apices of sterile shoots ..... *Tetraphis*
349. Peristome teeth 16; propagula cups absent 350
350. Leaves homomallous, broadly oblong to oblong-ovate, subacute to obtuse ..... *Aulacomnium*
350. Leaves not homomallous, oblong to lanceolate, mucronate to acuminate 351
351. Leaves broadly to narrowly lanceolate; peristome double ..... *Meesia*
351. Leaves broadly oblong to spatulate; peristome single 352
352. Costa in transverse section with 2 stereid bands ..... *Barbula*
352. Costa in transverse section with 1 stereid band ..... *Scopelophila*
353. Plants filiform, julaceous (if costa not excurrent see also *Anomobryum*) ..... *Aongstroemia*
353. Plants coarser, not julaceous 354
354. Capsules horizontal to pendulous 355
354. Capsules erect 360
355. Capsules curved, asymmetric 356
355. Capsules straight, symmetric 357
356. Exostome shorter than and alternate with endostome ... *Plagiobryum*
356. Exostome longer than and opposite to endostome ..... *Funaria*
357. Capsules ovoid, less than 1 mm long; stomates none; endostome fused to exostome, cilia none ..... *Discelium*
357. Capsules cylindric to ovoid, usually greater than 1 mm long; stomates present; endostome free of exostome, cilia mostly present 358
358. Leaf cells in oblique rows ..... *Plagiobryum*
358. Leaf cells not in obvious oblique rows 359
359. Leaf cells 4:1 or less ..... *Bryum*

359. Leaf cells 5:1 or longer ..... *Pohlia*
360. Peristome absent 361
360. Peristome present 363
361. Calyptrae 4-angled, sheathing the entire capsule until after dehiscence ..... *Pyramidula*
361. Calyptrae not angled, not sheathing or persistent 362
362. Capsules subcylindric or narrowly pyriform; annuli none; exothecial cells oblong to oblong-linear; calyptrae inflated-cucullate ..... *Entosthodon*
362. Capsules urceolate to broadly pyriform; annuli present; exothecial cells irregularly hexagonal; calyptrae inflated-mitrate ..... *Physcomitrium*
363. Peristome of endostome only, without a center line on the outer surface ..... *Mielichhoferia*
363. Peristome double or of exostome only, with a center line on the outer surface 364
364. Capsules with scarcely differentiated neck 365
364. Capsules with well-differentiated neck (apophysis) 366
365. Plants of arctic tundra ..... *Funaria*
365. Plants of British Columbia (50° N) and south ..... *Entosthodon*
366. Urns black, sometimes with yellow apophyses ..... *Tetraplodon*
366. Urns and apophyses green to brown 367
367. Setae pale greenish-white, slender; costa filling the acumen; plants of eastern North America ..... *Splachnum*
367. Setae brownish, stout to slender; costa ending below the leaf apex; plants of western and northern North America ..... *Tayloria*
368. Leaves conspicuously 4-ranked ..... *Conostomum*
368. Leaves not conspicuously ranked (if 3-ranked see *Meesia*) 369
369. Leaf cells short, 1(–2):1, rounded to quadrate 370
369. Leaf cells long, (3–)4:1 or longer, rectangular to long-hexagonal 386
370. Perichaetial leaves strongly differentiated, with an awn as long as the lamina; leaves bistratose ..... *Diphyscium*
370. Perichaetial leaves slightly or not differentiated, never long awned; leaves uni- to multistratose 371
371. Capsules distinctly 8 or 16 ribbed and furrowed 372
371. Capsules smooth or indistrictly furrowed when dry but without distinct ribs 378
372. Calyptrae mitrate 373
372. Calyptrae cucullate 375
373. Calyptrae hairy ..... *Ulota*
373. Calyptrae naked 374
374. Annuli none; calyptrae plicate ..... *Orthotrichum*
374. Annuli compound; calyptrae not plicate ..... *Brachydontium*
375. Setae cyneous; plants rare, forming tight cushions on alpine slopes ..... *Oreas*
375. Setae erect (but sometimes twisted); plants various but not as above 376
376. Capsules abruptly bent at the seta-capsule junction and horizontal, often becoming purple-red when mature ..... *Ceratodon*
376. Capsules erect to suberect and becoming brown when mature .. 377

377. Peristome teeth divided to half their length; capsules cylindric to ovoid-cylindric, ca. 2 mm long; plants of Pacific Northwest ..... *Cynodontium*
377. Peristome teeth undivided; capsules ovoid, less than 1 mm long; plants of eastern and midwestern U.S. and maritime Canada ..... *Rhabdoweisia*
378. Capsules with an erect, elongate, well defined neck; peristome double ..... *Meesia*
378. Capsules with a short, inconspicuous neck; peristome single 379
379. Capsules inclined 380
379. Capsules erect 381
380. Capsules less than 1 mm long, black, not strumose; leaf margins unistratose; plants of rich fens ..... *Catoscopium*
380. Capsules 1.5–2.0 mm long, pale, strumose; leaf margins bistratose; plants on moist soil, rocks and logs ..... *Oncophorus*
381. Capsules immersed to short-exserted ..... *Grimmia*
381. Capsules long-exserted 382
382. Calyptrae mitrate 383
382. Calyptrae cucullate, not plicate 384
383. Calyptrae plicate; setae straight ..... *Ptychomitrium*
383. Calyptrae not plicate; setae cygneous ..... *Campylostelium*
384. Costa with 1 stereid band; leaf margins bistratose ... *Trichostomopsis*
384. Costa with 2 stereid bands; leaf margins unistratose 385
385. Leaves lanceolate from a somewhat expanded base ..... *Didymodon*
385. Leaves oblong ..... *Barbula*
386. Leaves subulate 387
386. Leaves acute to acuminate 394
387. Capsules curved and asymmetric ..... *Dicranella*
387. Capsules straight, symmetric, although sometimes inclined to pendulous 388
388. Setae flexuose-curved to cygneous 389
388. Setae straight, but sometimes spirally-twisted 391
389. Setae more 10 mm long; plants more than 5 mm tall; leaves more than 4 mm long; capsules pyriform ..... *Leptobryum*
389. Setae less than 5 mm long; plants less than 3 mm tall; leaves less than 2 mm long; capsules hemispheric 390
390. Plants ephemeral, on soil in Florida; setae stout, curved at apex, not twisted; capsules eperistomate ..... *Eccremidium*
390. Plants perennial, on rock, not in Florida; setae slender, twisted; capsules peristomate ..... *Seligeria*
391. Peristome double; plants arctic ..... *Pseudoditrichum*
391. Peristome single; plants widespread 392
392. Capsules ovoid; plants on calcareous rocks ..... *Seligeria*
392. Capsules oblong to cylindric; plants generally on soil 393
393. Capsules long cylindric; peristome teeth divided to base, terete, papillose ..... *Ditrichum*
393. Capsules short cylindric; peristome teeth divided half their length, flat, vertically pitted-striolate ..... *Dicranella*
394. Costa occupying ½ or more of leaf base; capsules curved and asymmetric, elongate-pyriform from a neck as long as the urn ..... *Amblyodon*

394. Costa occupying less than ¼ the leaf base; capsules straight and symmetric, without conspicuous neck 395
395. Plants small, less than 2 mm high, gregarious, occurring on calcareous rocks; capsules ovoid ..... *Seligeria*
395. Plants larger, mostly more than 5 mm, in tufts occurring on various substrates; capsules cylindric 396
396. Leaves flexuose-twisted when dry; capsules erect; plants occurring in the southern Appalachians and California ..... *Orthodontium*
396. Leaves erect, little altered when dry; capsules erect or inclined; plants widespread 397
397. Capsules terminal, inclined to pendent; peristome double; leaves usually more than 1 mm long, sometimes with axillary propagula ..... *Pohlia*
397. Capsules appearing lateral, erect; peristome single; leaves less than 1 mm long, never with propagula ..... *Mielichhoferia*
398. Leaves bistratose throughout, ligulate to oblong, obtuse; perichaetial leaves long awned ..... *Diphyscium*
398. Leaves unistratose, or if bistratose then not ligulate to oblong; perichaetial leaves not so differentiated 399
399. Leaf cells rectangular, prorulose; capsules globose, rugulose to furrowed when dry 400
399. Leaf cells rounded-quadrate, uni- to pluripapillose; capsules ovoid to cylindric, smooth or furrowed 403
400. Leaves strongly ranked ..... *Conostomum*
400. Leaves not conspicuously ranked 401
401. Capsules erect, or if pendent then from curvature of seta, symmetric, rugulose when dry; peristome reduced to a low membrane .. *Bartramidula*
401. Capsules strongly inclined, asymmetric, furrowed; peristome better developed 402
402. Leaves unistratose; plants on soil and rocks in at least periodically wet habitats, often with innovative branches beneath inflorescences ..... *Philonotis*
402. Leaves bistratose at least at margins; plants on banks and cliffs in mesic habitats, without innovative branches ..... *Bartramia*
403. Leaf cells appearing papillose from slightly thickened walls between cells (not prorulose) 404
403. Leaf cells papillose over the lumina 405
404. Leaves crispate when dry; capsules long exserted, cylindric; plants usually occurring on logs ..... *Dicranoweisia*
404. Leaves erect, straight to curved; capsules immersed to short exserted, ovoid-cylindric; plants occurring on rocks ..... *Grimmia*
405. Leaf cells collenchymatous and stellate 406
405. Leaf cells not thickened in the corners or if so merely rounded and not stellate 407
406. Leaf cells unipapillose; leaves not recurved ..... *Aulacomnium*
406. Leaf cells pluripapillose; leaves recurved ..... *Geheebia*
407. Leaves with abruptly differentiated hyaline cells occupying most of the leaf base (cancellinae) and with an intramarginal border of elongate cells (teniolae), at least in lower part of leaf; usually with propagula on leaf apex ..... *Calymperes*

407. Leaves without cancellinae, of if present then never with teniolae; propagula never on leaf apices but sometimes elsewhere on leaves or in axils 408
408. Plants with propagula borne terminally on specialized stalks from stem apices ..... *Aulacomnium*
408. Plants with or without various means of asexual reproduction but these never borne on stalks from the stem apices 409
409. Plants occurring on tree trunks or bare rock, with immersed to shortly exserted, often ribbed capsules 410
409. Plants usually occurring on soil, if on rocks or trees then capsules long exserted and mostly unribbed (or plants sterile) 412
410. Calyptrae cucullate, not plicate, naked; plants occurring on wet rocks ..... *Amphidium*
410. Calyptrae mitrate, plicate, usually hairy; plants occurring on tree trunks and dry rocks 411
411. Leaves usually crispate to contorted when dry; basal marginal cells with thickened transverse walls; stomates superficial; capsules shortly exserted ..... *Ulota*
411. Leaves usually little altered when dry; basal marginal cells not differentiated; stomates immersed or superficial; capsules immersed to shortly exserted ..... *Orthotrichum*
412. Costa in transverse-section more or less homogeneous, without differentiated stereids 413
412. Costa in transverse-section with differentiated stereid bands 417
413. Leaf cells with C-shaped papillae; leaves broadly spatulate ..... *Gymnostomiella*
413. Leaf cells with simple, conic papillae; leaves various but not broadly spatulate 414
414. Upper leaf cells with 4–7 small, conic papillae ..... *Zygodon*
414. Upper leaf cells with 3 or fewer, simple to branched papillae ... 415
415. Leaves less than 0.6 mm long, ligulate, rounded-obtuse; rare plants of calcareous rocks; annuli of 2–3 rows of well-differentiated cells ..... *Gyroweisia*
415. Leaves more than (0.7–)1.5 mm long, lanceolate to ovate, acuminate to obtuse; annuli poorly differentiated 416
416. Leaves typically crispate to contorted when dry; basal marginal cells with thickened transverse walls; capsules shortly exserted; calyptrae hairy ..... *Ulota*
416. Leaves usually little altered when dry; basal marginal cells not differentiated; capsules immersed to shortly exserted; calyptrae naked (species with contorted leaves) to hairy (species with unaltered leaves) ..... *Orthotrichum*
417. Costa with a single, dorsal stereid band 418
417. Costa with both dorsal and ventral stereid bands 429
418. Calyptrae campanulate-mitrate, covering entire capsule, often lobed at base; basal leaf cells with thickened transverse walls ..... *Encalypta*
418. Calyptrae cucullate, covering only operculum and capsule apex, unlobed at base; basal leaf cells usually without thickened transverse walls 419

419. Leaves linear-lanceolate to lanceolate, never with hair points; leaf margins recurved to plane; leaf cells with papillae conic, clavate or branched, rarely C-shaped 420
419. Leaves broadly lanceolate (from revolute leaf margins), lingulate or oblong-ovate, sometimes with hair points; leaf margins recurved to strongly revolute; leaf cells with papillae stellate from a stipitate base to C-shaped 424
    420. Leaf cells with 4–7 widely spaced, small, conic papillae; elliptic propagula present in leaf axils; peristome double; plants usually occurring on trees, rarely on rock ..... *Zygodon*
    420. Leaf cells with 1–3(–4) closely set, simple to branched papillae; propagula absent; peristome single or absent; plants occurring on soil and rocks 421
421. Leaf margins serrulate above; capsules erect to inclined, often furrowed and strumose; peristome vertically pitted-striolate ..... *Cynodontium*
421. Leaf margins entire; capsules erect, never furrowed or strumose; peristome, when present, papillose 422
    422. Basal leaf cells lax and hyaline; upper leaf margins bistratose throughout; peristome present ..... *Trichostomopsis*
    422. Basal leaf cells firm-walled, pale but not hyaline; upper leaf margins unistratose or irregularly bistratose; peristome absent 423
423. Stem monopodially branched; archegonia on short, lateral branches; stem transverse section rounded-triangular ..... *Anoectangium*
423. Stem sympodially branched; archegonia terminal on main stem; stem transverse section round ..... *Gymnostomum*
    424. Leaves with an intramarginal band of enlarged, smooth, often orange cells ..... *Crumia*
    424. Leaves without differentiated intramarginal cells but sometimes with smooth marginal cells, these not enlarged 425
425. Leaves narrowly lanceolate; leaf margins erect and bistratose ..... *Trichostomopsis*
425. Leaves oblong, lingulate to ovate; leaf margins plane to revolute, unistratose or if bistratose then always revolute 426
    426. Upper leaf margins broadly revolute to spirally revolute, with cells often more strongly chlorophyllose than median cells ..... *Pseudocrossidium*
    426. Upper leaf margins plane to revolute, with cells undifferentiated or paler than median cells 427
427. Leaves unbordered; peristome none or rudimentary ..... *Pottia*
427. Leaves often bordered by smooth cells; peristome present 428
    428. Peristome teeth united in a high or rarely low, tubular basal membrane, spirally twisted above; cells of adaxial (upper) surface of costa similar to or smaller than laminal cells in transverse section ..... *Tortula*
    428. Peristome teeth free or rarely united in a low basal membrane, erect to slightly twisted above; cells of adaxial surface of costa mostly larger than or otherwise differentiated from laminal cells in transverse section ..... *Desmatodon*
429. Leaf margins abruptly serrate at the shoulder ..... *Eucladium*
429. Leaf margins entire at shoulders 430

430. Leaf cells with numerous (more than 7), minute, elliptic papillae over the walls as well as the lumina ..... *Amphidium*
430. Leaf cells with fewer than 7, larger, round papillae only over the lumina 431
431. Leaf margins toothed above 432
431. Leaf margins entire or roughened with projecting papillae 436
432. Laminae bistratose; margins unistratose ..... *Rhexophyllum*
432. Laminae unistratose; margins uni- or bistratose 433
433. Leaf cells bulging, mammillose to unipapillose ..... *Dichodontium*
433. Leaf cells plane, pluripapillose 434
434. Stems with central strand ..... *Bryoerythrophyllum*
434. Stems without central strand 435
435. Stems with hyalodermis; adaxial (upper) surface of costa with enlarged, papillose epidermal cells ..... *Paraleptodontium*
435. Stems without hyalodermis; adaxial surface of costa with small, smooth cells ..... *Leptodontium*
436. Leaves at extreme apex with large, curved, projecting papillae ..... *Dichodontium*
436. Leaves at extreme apex with margins entire or papillose-crenulate 437
437. Stems triquetrous, especially when moist; leaf cells unipapillose, the papillae sometimes branched; plants of California ..... *Triquetrella*
437. Stems without ranked leaves; leaf cells pluripapillose; plants widespread 438
438. Stems without central strand, in transverse section with largest cells in middle of section ..... *Oxystegus*
438. Stems with central strand, or if poorly developed at least in transverse section with largest cells not in middle of stem 439
439. Leaf margins plane to erect 440
439. Leaf margins recurved to revolute, at least near midleaf or below 443
440. Stems with hyalodermis ..... *Trichostomum*
440. Stems without hyalodermis, epidermal cells small 441
441. Leaf apices subtubulose; upper leaf cells with 1–2 large, centered, multiplex papillae ..... *Tuerckheimia*
441. Leaf apices flat; upper leaf cells with 3–6 small, scattered, simple, blunt papillae 442
442. Perichaetia and sporophytes lateral; leaves 2.2–3.0 mm long; axillary hairs of 15–20 cells ..... *Molendoa*
442. Perichaetia and sporophytes terminal; leaves less than 2.0 mm long; axillary hairs of 8–10 cells ..... *Gymnostomum*
443. Peristome none; leaves recurved only on one side ..... *Hymenostylium*
443. Peristome usually present; leaves recurved on both sides 444
444. Axillary hairs with a brown, slender basal cell; laminal cells well defined in surface view; leaves usually lanceolate; cells of abaxial (back) surface of costa quadrate to short-oblong, rarely elongate; basal laminal cells usually little differentiated, green and short-rectangular ..... *Didymodon*
444. Axillary hairs with all cells hyaline; laminal cells obscure in surface view; leaves usually ovate to oblong; cells of abaxial surface of costa

oblong to elongate; basal laminal cells usually strongly differentiated, hyaline and elongate ..... *Barbula*

ACKNOWLEDGMENTS

We thank the Natural Sciences and Engineering Research Council of Canada for support of this research, both indirectly through the support of previous field work and laboratory research of D.H.V. and directly by monies that allowed us to work together in Edmonton for a period of time. We also thank Sandra Vitt who provided significant help in organizing our primitive attempts in the use of computers. Willam D. Reese carefully read a draft of this key and made numerous comments for which we are grateful.

LITERATURE CITED

Anderson, L. E. 1990. A checklist of *Sphagnum* in North America north of Mexico. Bryologist 93: 500, 501.

Anderson, L. E., H. A. Crum and W. R. Buck. 1990. List of mosses of North America north of Mexico. Bryologist 93: 448–499.

Corley, M. F. V., A. C. Crundwell, R. Düll, M. O. Hill and A. J. E. Smith. 1981. Mosses of Europe and the Azores; an annotated list of species, with synonyms from the recent literature. J. Bryol. 11: 609–689.

Crum, H. A. 1973. Mosses of the Great Lakes Forest. Contr. Univ. Michigan Herb. 10: 1–404. [3rd edition, 1983.]

Crum, H. A. and L. E. Anderson. 1981. *Mosses of Eastern North America.* Volumes 1 and 2. Columbia University Press, NY. 1328 pp.

Flowers, S. 1973. *Mosses: Utah and the West.* Brigham Young University Press. Provo, UT. 567 pp.

Grout, A.J. 1931–1940. *Moss Flora of North America North of Mexico.* Volumes I–III. Published by the author, Newfane, Vermont and New York. 264, 285 and 275 pp.

Ireland, R. R. 1982. *Moss Flora of the Maritime Provinces.* National Museums of Canada Publications in Botany No. 13. Ottawa. 738 pp.

Ireland, R.R., G.R. Brassard, W. B. Schofield and D. H. Vitt. 1987. Checklist of the mosses of Canada II. Lindbergia 13: 1–62.

Lawton, E. 1971. *Moss Flora of the Pacific Northwest.* Hattori Botanical Laboratory, Nichinan, Japan. 362 pp. + 195 plates.

Lesquereux, L. and T. P. James. 1884. *Manual of the Mosses of North America.* S. E. Cassino, Boston. 447 pp.

Magill, R. E. 1990. *Glossarium Polyglottum Bryologiae: A Multilingual Glossary for Bryology.* Monographs in Systematic Botany from the Missouri Botanical Garden. Vol. 33. 297 pp.

Murray, B. M. 1988. Systematics of the Andreaeopsida (Bryophyta): Two orders with links to *Takakia.* Beih. Nova Hedwigia 90: 289–336.

Redfearn, P. L., Jr. 1972. Mosses of the Interior Highlands of North America. Ann. Missouri Bot. Gar. 59: 1–104. [Reprinted with changes and additions, 1983.]

Reese, W.D. 1984. *Mosses of the Gulf South from the Rio Grande to the Apalachicola.* Louisiana State University Press, Baton Rouge, LA. 252 pp.

Smith, D. K., K. D. McFarland and P. G. Davidson. 1990. *Takakia,* nanjamonja-goke: Characteristics of the sporophyte and reconsideration of classification. Abstract, p. 22: American Bryological and Lichenological Society, 1990 meeting, Wakulla Springs, Florida.

Vitt, D. H., J. E. Marsh and R. B. Bovey. 1988. *Mosses Lichens & Ferns of Northwest North America.* Lone Pine Press, Edmonton, AB and The Univeristy of Washington Press, Seattle, WA. 296 pp.

Contr. Univ. Mich. Herb. 18:73–86. 1992.

A CONTRIBUTION TOWARD A HISTORY OF THE ARCTIC MOSS FLORA

Norton G. Miller
Biological Survey, New York State Museum
Albany, NY 12230, U.S.A.

INTRODUCTION

The existence of a unique group of bryophytes occurring largely in the circumarctic region north of the tree line was recognized by Steere (1953, 1965) who considered them to be representatives of a High Arctic Floristic Element. He postulated that the species had once belonged to a "widely distributed Tertiary flora now restricted to unglaciated arctic areas by continental glaciation at lower latitudes" (1969, p. 510).

I show here that some high-arctic mosses, together with other species of a more general far northern distribution, in fact were present in midcontinent North America at about 40° North Latitude as recently as 20,000 radiocarbon years ago (yr B.P.), i.e., at or several thousand years before the onset of retreat from the maximum position attained by the Wisconsinan Laurentide ice sheet. These full-glacial paleobryofloras are about 10,000 years older than the more completely documented late-glacial moss floras that existed in the Great Lakes–New England region at about 11,000 yr B.P. (Miller 1984). The glacial maximum floras indicate that open, tundralike vegetation prevailed when the fossils were buried. Species of both upland, well-drained sites and wetlands are represented. I suggest that these ancient southern occurrences of mosses of present arctic distribution were the result of dispersal rather than the remnants of the pre-Pleistocene flora. Thus midcontinent North America and regions to the east and west along the limit of continental glaciation may have been a center of dispersal for the arctic flora, joining unglaciated Beringia, parts of the Arctic Archipelago, and other northern refugia as potential source areas for plants migrating into the North American Arctic during the late Quaternary.

The phytogeography of mosses and hepatics has been an enduring topic of inquiry to which Howard Crum (1972), whom we honor in this Festschrift, and many others in North America (e.g., Schofield 1969; Schofield and Crum 1972; Steere 1965; Schuster 1983) have made significant contributions. This body of work has influenced the theory and practice of bryophyte systematics and investigations into the evolutionary biology of bryophytes. In most phytogeographical studies bryologists have emphasized the analysis and interpretation of existing distributional areas. However, attempts to trace the origins of floras have been weakened by the absence of information on the occurrence of species through time. This is mainly because there may be only a slight correspondence between the present and past distributions of a given species. But there is an excellent source of data about past distributions because the Quaternary fossil record of the mosses of glaciated regions is very rich, as studies by paleobotanists and paleoecologists have repeatedly demonstrated over the past two decades. Therefore, opportunities for new phytogeographical syntheses will result as the paleobotanical record is integrated

with what is known about the distribution of the extant flora. I recommend that future phytogeographical studies be designed to gather original data about fossil mosses, and that existing data about fossil bryophytes be utilized in analyses of the patterns of distribution.

Fossil mosses are convenient subjects in studies of historical plant geography for several reasons. Isolated and cleaned of associated sediment, they can be dissected, sectioned, and mounted for examination under a microscope much as one would a fresh sample of moss plants. Preservation is sometimes incomplete, owing to degradation caused by one or a number of possible biological or physical processes, or cellular details may be obscured by the deposition of iron pyrite or other minerals. In general, however, fossils of mosses are easy to work with, and during the identification process one soon learns what diagnostic characters to evaluate against those of the reference specimens. Moreover, the Quaternary moss record appears to be characterized by little or no extinction, or at least no fossils of extinct species have yet been adequately documented. Procedures used in the study of Quaternary bryophyte fossils are summarized by Janssens (1990) and Miller (1990).

I report here on my continuing studies of moss fossils from Pleistocene deposits in Illinois, Ohio, and nearby regions that are associated with deposits marking the farthest extension of the late-Wisconsinan glaciation. This research has included analyses of other plant fossils, such as pollen and the remains of vascular plants, the results of which were obtained in collaboration with colleagues and will be presented more fully elsewhere. I briefly review these data to provide information on the paleoenvironmental settings of the floras. However, the emphasis of this paper is on phytogeography and in particular the history of the arctic moss flora.

SITE DESCRIPTIONS

The location of the fossil beds (Fig. 1), a short description of the stratigraphy at each of the sites, and radiocarbon dates pertinent to the age of moss fossils are given below.

1. Clinton Power Station Site, De Witt County, Illinois, 8 km east of Clinton. Buried moss peat was discovered during excavations resulting from the construction of a nuclear power station. The 1–2-cm-thick moss bed occurred beneath loess (1.5 m), tills of the Wedron Formation (9.4 m), and clay (0.1 m) (measurements from surface) and above 0.9 m of Morton loess. The age of the moss peat was 20,670 ± 280 yr. B.P. (ISGS-828). The stratigraphic information and samples of the peat were sent to me by James E. King, then of the Illinois State Museum, Springfield.

2. Sharonville Site, Hamilton County, Ohio, 1.5 km southeast of Sharonville. A 2–3-cm-thick layer of peat, interpreted as A_o paleosol and marking the upper limit of a deposit of organic-rich silt of variable thickness (to 50 cm), is exposed along a tributary of Mill Creek for a distance of approximately 8 m. Above the organic bed is 0–40 cm of clay, and above this is compact diamicton (till). The geology of the site is described more completely by Lowell *et al.* (1990b). They report the age of the organic bed as 21,120 ± 130 yr. B.P. (PITT-0225) and also give 19,670 ± 68 yr. B.P. as the average of five age determinations of wood from a cluster of four tamarack stumps in growth position at the top of the organic silt. The average is taken as the age of the area when it was overriden by the continental ice margin. Mosses were extracted from a sample consisting of the peat and the sediments immediately

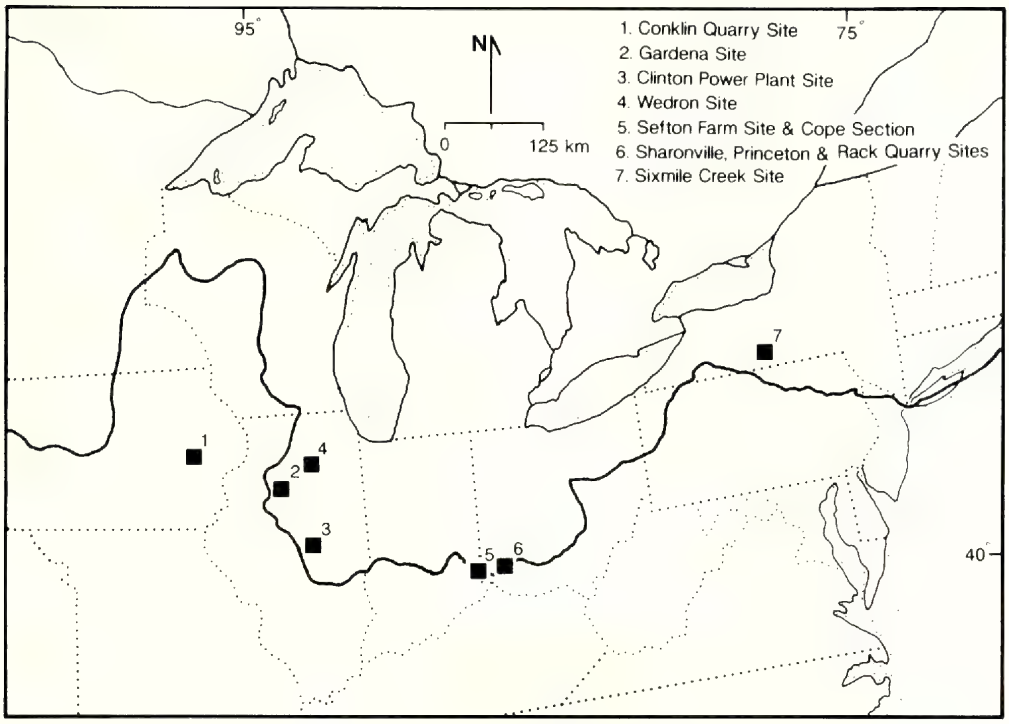


FIG. 1. Map of central and eastern North America showing location of full-glacial paleobotanical sites mentioned in text and approximate limit of Wisconsinan glaciation (dark line).

above and below (KS-87-09-AA). The sample was collected by Thomas Lowell and Kevin Savage, Department of Geology, University of Cincinnati.

3. Princeton Sewage Treatment Plant Site, Hamilton County, Ohio, 1 km northeast of Glendale. Excavations associated with expansion of the plant revealed a thin continuous peat bed over a deposit of organic silt, beneath (from top) diamicton (3 m) and a layer of silt (0.25 m), with discontinuous clay-rich zones in contact with the peat. Two samples from the southwest corner of the excavation (TL-87-214-AA and TL-87-214-CC) yielded the moss fossils reported here. From a third sample (TL-87-214-DD) a small twig, probably of willow (*Salix* sp.), was removed from the peat, cleaned, and dated, using accelerator mass spectrometry (AMS). Its age was 19,135 ± 160 yr. B.P. (Beta-34385, ETH-6063).

4. Rack Sand Quarry Site, Hamilton County, Ohio, 8 km north of the business center of Cincinnati. A peat bed, 0.4–0.5 m thick, exposed on the north wall of the quarry was sampled for pollen and bryophytes on my behalf during the summer of 1988 by Jerry Snider, Department of Biological Sciences, University of Cincinnati. The geology, paleobotany, and paleontology of the site are being investigated by Thomas Lowell, Kevin Savage, and other colleagues (Lowell *et al.* 1990a). The peat overlies a dense clay and is itself overlain by about 5 m of clay that contains silt interbeds and lenses. The upper 2–2.5 m of the topmost clay is oxidized, indicating that it is weathered. The radiocarbon age of a small twig from near the bottom of the peat was 20,230 ± 300 yr B.P. (Beta-33944, ETH-5951), and a second twig from the clay just above the peat was 19,060 ± 265 yr B.P. (Beta-33943, ETH-5950). These ages were obtained by the AMS method. A third age (Lowell *et al.* 1990a), obtained by conventional radiocarbon analysis of wood from the peat, was 19,470 ± 115 (PITT-0510).

METHODS

Sediment samples containing moss fossils were soaked in 5% Na_2CO_3 in beakers until the sediment disaggregated. Some samples required soaking for 14 hours or longer in warm (70°C) Na_2CO_3. The sediment chunks were gently pulled apart by hand to avoid degrading the fossils. Samples consisting of more than one type of sediment, for example, lower clay–peat–upper clay sequences, were separated into uniform subsamples that were treated separately. When the sediment had been reduced to a slurry, it was poured into a 250-μm-mesh sieve through which small particles then were washed with tapwater. Residues retained on the mesh were soaked in distilled water for 24 hours or until the water remained clear after standing for an hour or more, and then were examined microscopically. The fossils were sorted and identified, and stems and leaves were sectioned when necessary. A set of the fossils mounted in Hoyer's solution has been deposited in the Quaternary Paleobotany Collection of the New York State Museum.

RESULTS

To place each of the fossil moss assemblages in a paleoenvironmental context, results of pollen and plant macrofossils analysis are described and interpreted briefly.

Clinton. The pollen assemblage in the moss peat (counted by J. E. King) is dominated by pine and sedge pollen, the latter accounting for 62% of the total. Excluding sedge pollen (which presumably originated mostly from wetland plants growing in the depositional basin), pine (59%) and grass (18%) are the principal pollen types, with spruce (4%), birch (3%), willow (2%), and ragweed (7%) present in low amounts. Together, the six pollen types amount to 93% of the assemblage. These data and the low influx of total pollen (estimated at 821 grains/cm^2/yr under the assumption that the peat accumulated in 40 years; cf. radiocarbon dates and peat thickness for Rack) indicate that treeless landscapes occurred nearby under climatic conditions similar to those at places in the contemporary Arctic where low pollen influx has been registered.

Sharonville. Pollen counts by S. T. Jackson revealed a moderately high sedge total (18% when Cyperaceae were included in the percentage base). With sedges excluded the principal pollen types were spruce (41%), pine (36%), grass (8%), and Compositae (7%, including 1% ragweed). These account for 92% of the assemblage. Needles (spruce), wood (spruce, larch), and twigs (*Juniperus horizontalis*) are present in the moss peat. The pollen and macrofossils indicate an open landscape, with spruce and tamarack in scattered stands and interspersed open, dry or mesic sites in which light-demanding mosses and shrubs grew (Miller and Jackson 1989).

Princeton. The moss peat contained a higher percentage of sedge pollen (40% when Cyperaceae were included in the percentage base) than at Sharonville. Other components (with sedge pollen excluded from the calculations) were spruce (37%), pine (37%), grass (12%), *Thalictrum* (5%), and Compositae (3%, including 1% ragweed). Most (95%) of the pollen assemblage is distributed among these five categories. Small willow stems with buds and one spruce seed occurred in the moss peat, but no spruce needles were recovered; this contrasts with the Sharonville peat in which they were abundant. The similarities and contrasts between the Sharon-

TABLE 1. Composition of full-glacial moss floras represented in buried peats from sites in Illinois and Ohio (see text).

	Clinton	Sharonville	Princeton		Rack
			214-AA	214-CC	
Amblystegium serpens	.	.	.	X	.
Brachythecium turgidum	X	.	.	X	.
Bryum neodamense	X	.	.	.	X
B. pseudotriquetrum	X	.	X	X	X
B. sp[1]	.	X	.	.	.
Calliergon giganteum	X	.	.	.	X
Campylium chrysophyllum	.	X	X	X	.
C. stellatum	X	.	.	X	X
Cinclidium latifolium	X	.	.	.	.
C. stygium	.	.	.	.	X
Cratoneuron filicinum	.	.	X	X	.
Dicranella sp.	.	X	.	.	.
Didymodon asperifolius	.	.	X	X	.
Ditrichum flexicaule	.	.	X	X	.
Drepanocladus aduncus	X	.	.	.	.
D. brevifolius	.	.	X	.	.
D. revolvens	X	.	.	.	X
D. uncinatus	.	X	.	.	.
Hypnum lindbergii	X	.	.	.	.
Meesia triquetra	.	.	.	.	X
Polytrichum commune	X	.	.	.	.
Scorpidium scorpioides	.	.	.	.	X
Thuidium abietinum	.	X	X	X	.
Tortula norvegica	.	.	X	X	.
Totals	10	5	8	10	8

[1]A third but unidentifiable species of *Bryum*.

ville and Princeton records indicate that trees were absent or very sparse locally at Princeton (Miller and Jackson 1989), or if some were present, that conditions were not appropriate for preservation of their remains.

Rack. Seven stratigraphically separated samples from a 30 cm section of moss peat (sample interval 3–5 cm) yielded pollen assemblages dominated by sedge, spruce, and pine. Sedge representation varied from 17–48% ($\bar{x}$ = 37%), with Cyperaceae totals included in the percentage calculations. Data for other principal types (with sedge excluded from the percentage base) were spruce 42–56% ($\bar{x}$ = 47%), pine 29–42% ($\bar{x}$ = 35%), oak 1–4% ($\bar{x}$ = 2%), grass 3–8% ($\bar{x}$ = 4%), and Compositae 1–5% ($\bar{x}$ = 3%). These types accounted for over 90% of each pollen assemblage. Total pollen influx appears to have been very low, 400–1122 grains/cm^2/yr ($\bar{x}$ = 806) and similar to results obtained for the Clinton moss peat. The low pollen deposition rates at Clinton and Rack indicate an open, tundralike vegetation, with trees and other plants that produce abundant, well-dispersed pollen located at places distant from the moss beds.

Mosses. Samples of the peat beds at the four sites yielded plants of 24 species of mosses (TABLE 1). Most (16) were represented in only one of the fossil beds. Two mosses, *Bryum pseudotriquetrum* and *Campylium stellatum* were present at three of the four sites, but no moss was a member of all four assemblages. The sites contained fossils of five, eight, or 11 species.

The fossils were well preserved in all samples, and numerous fragments were

TABLE 2. Percent-composition of fossil moss assemblages in four samples of the peat bed at Rack Quarry, Hamilton County, Ohio.

species/sample number	1	2	3	4
Scorpidium scorpioides	35	30	35	30
Drepanocladus revolvens	35	25	30	30
Meesia triquetra	5	30	30	5
Campylium stellatum	20	–	–	25
Cinclidium stygium	t	5	t	5
Calliergon giganteum	5	–	t	5
Bryum neodamense	–	10	5	–
B. pseudotriquetum	t	–	–	–
Number of species	7	5	6	6

t = trace

recovered for most species. For the fossils that could be identified only to genus (*Bryum, Dicranella*), either sporophytes were absent or too little plant material was available to reveal diagnostic characteristics.

Replicate samples from Princeton (TABLE 1) and Rack (TABLE 2) were studied to compare the representation of species in the peats. The two samples from Princeton were 1 m apart and together yielded fossils of 11 mosses. Seven species were represented in both samples, and four were in one but not the other, with three unique to sample CC and one to AA. The four samples from Rack were from a 25 cm^2 area, and both species presence and values for percent composition were determined. For the latter a subsample was removed from each sample and sorted into components. A visual estimate of the area occupied by each component was taken, using centimeter graph paper. Fossils of eight species were present in the four samples, but no single sample had all eight. The totals varied from five to seven (TABLE 2). There was also considerable variation in the composition of the four assemblages, but the leading species were *Scorpidium scorpioides, Drepanocladus revolvens,* and *Meesia triquetra.* Five species were present in trace amounts or were absent from some of the subsamples.

DISCUSSION

Before beginning a phytogeographical analyses of fossil moss assemblages, it is useful to interpret and summarize the paleoenvironments existing at the time the fossils were deposited. The four moss beds appear to have been buried by silt and clay, with little or no predepositional transport of the fossils. The best evidence for this conclusion is that the species mixtures are comparable in composition to extant bryophyte communities. At Clinton and Rack the mosses are indicative of rich-fen peatland systems, which develop in association with standing calcareous ground water and are typically dominated by brown mosses. At Rack a rich fen existed for 1200 radiocarbon years under what appear to have been unvarying environmental conditions, as indicated by the more or less uniform pollen spectra across the 30-cm-stratigraphic interval. The deposition of clay from a lake, probably the result of a rise in the water table caused by glacier advance, buried the mosses at Clinton and Rack. In contrast the Princeton and Sharonville assemblages are dominated by mosses of upland, well-drained or mesic habitats, such as an area with microscale relief consisting of a mosaic of sites from the tops of soil mounds to less well-drained

interswales and edaphically intermediate topography. At Sharonville the mosses appear to have been buried by silt or clay deposited from a lake; at Princeton perhaps by wind-blown silt (loess). The fossil assemblages at both places indicate *in situ* burial with little or no mixing of plants derived from substantially different contemporary moss communities, for example, those of wet versus dry habitats.

The full-glacial vegetation of parts of the North American Middle West, especially in Ohio where logs have been frequently found in late-Wisconsinan tills, has been interpreted as forest (Burns 1958; Goldthwait 1958; see also Wright 1981) or tree line tundra, with stands of trees and extensive open areas (Martin 1959). More recently, information has become available that strongly favors the latter interpretation. This includes the results of studies at Conklin Quarry (southeastern Iowa; Baker *et al.* 1986), Biggsville (northwestern Illinois; Baker *et al.* 1989), the Athens North Quarry and Gardena sites (central Illinois; F. King 1979; J. King 1979), and Wedron (northeastern Illinois; Garry *et al.* 1990), as well as data from the Clinton, Sharonville, Princeton, and Rack sites (Lowell *et al.* 1990a; Miller and Jackson 1989). When long records are available, for example at Biggsville and Athens North Quarry, there is evidence of a transition from spruce-pine forest (28,000–25,000 yr B.P.) to more open spruce-tamarack forest that lasted until 22,500 yr B.P. (Garry *et al.* 1990). This change was presumably in response to the gradual onset of glacial conditions, which culminated with the invasion of the continental ice margin circa 20,500 to 19,000 yr B.P. in the Illinois/Ohio region. Although evidence is scant for the time between 22,500 yr B.P. and the glacial maximum, available data indicate continued change toward more open landscapes such as those documented by fossils in the Clinton, Sharonville, Princeton, and Rack moss peats. Of these four records, only the Sharonville peat contains spruce needles and larch wood, indicating local presence of spruce and tamarack trees. Moss peats at the four sites contain mainly spruce, pine, and sedge pollen, but the influx values indicate distant sources for spruce and pine. The best working interpretation of the data now available is that full-glacial landscapes in midcontinent North America were open but that trees (spruce and tamarack) occurred at some places, producing together a pattern similar to that along the tree line in northern Canada where open tundra and stands of spruce and tamarack are intermingled.

Phytogeography. The four moss florules described here (Table 1) consist of species that are mostly broadly northern in distribution, with many now widespread in the northern United States (and sometimes southward in the mountains), through boreal Canada, and into the Subarctic and Arctic. Examples are *Cinclidium stygium* (Fig. 2; range mapped by Mogensen 1973) and *Meesia triquetra* (range mapped by Montagnes 1990). In contrast to the North American late-glacial moss flora (Miller 1976) few southern species appear to be represented in the full-glacial sites. An exception is *Campylium chrysophyllum,* which is distributed mainly in areas of deciduous forest or mixed conifer-deciduous forest, and which is recorded from Princeton.

Thirteen species in addition to the 24 mosses listed in Table 1 have been reported from the following full-glacial deposits in the central United States: Conklin Quarry, Iowa (Baker *et al.* 1986; Janssens and Baker 1984)—*Barbula fallax, Brachythecium reflexum, Distichium* cf. *capillaceum, Drepanocladus vernicosus, Hygrohypnum luridum,* and *Tomentypnum nitens;* Gardena, Illinois (J. King 1979; Miller 1979, with additions recorded here)—*Hypnum lindbergii, Plagiomnium medium* subsp. *curvatulum* (reported as *Mnium* (*Plagiomnium*) cf. *rugicum* by Miller 1979; revision by G. S. Mogensen), and *Scorpidium turgescens;* Wedron,

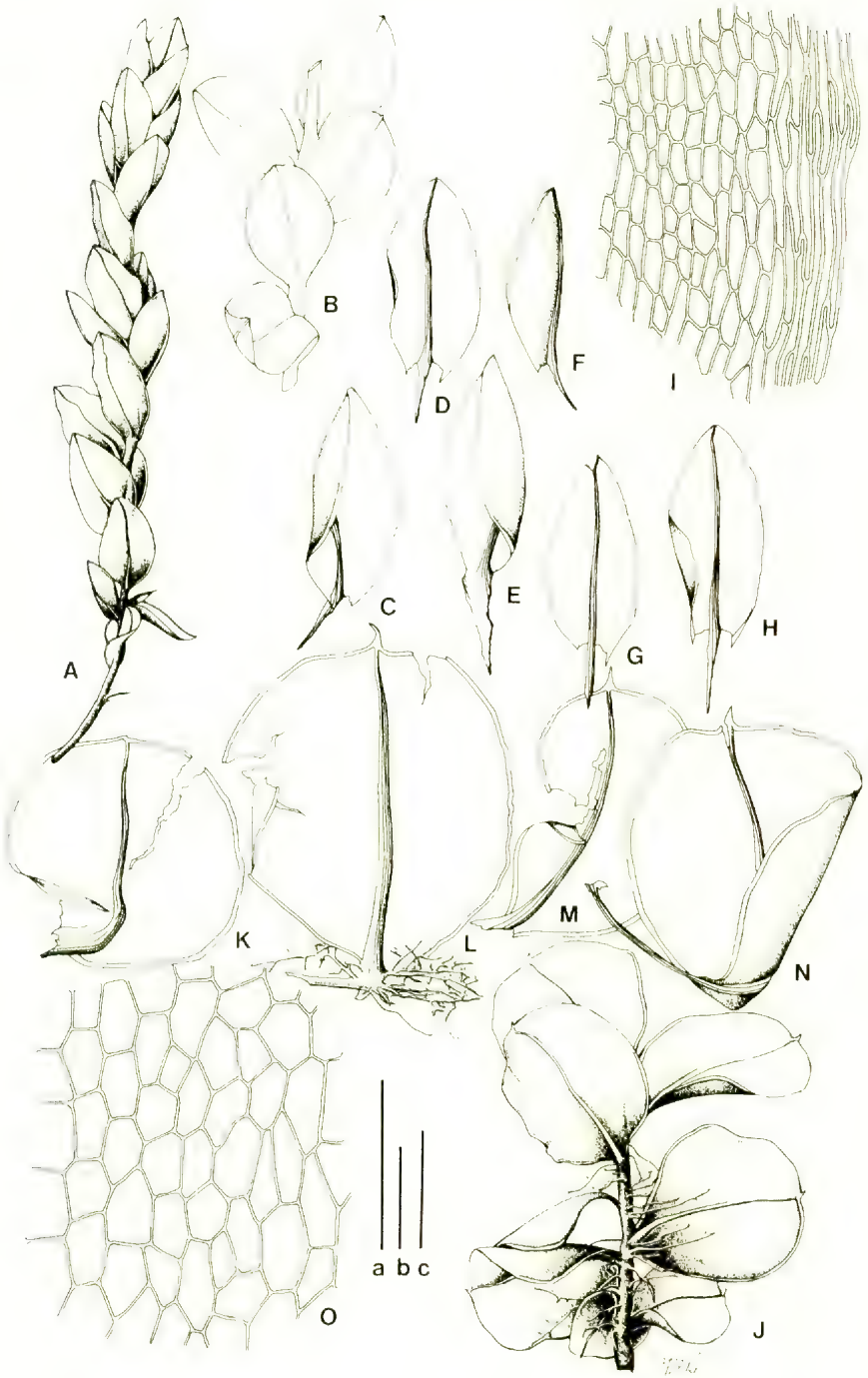


FIG. 2. Full-glacial fossil mosses from the Rack Quarry Site, Cincinnati, Ohio. A–I. *Bryum neodamense*. A. Habit (scale bar a). B. Portion of stem with leaves (a). C–H. Leaves showing short decurrencies (b). I. Cells at leaf margin (c). J–O. *Cinclidium stygium*. J. Habit (a). K–N. Leaves (b). O. Median laminal leaf cells (c). Scale bars: a = 3 mm, b = 1 mm, c = 100 μm. Drawings by Patricia M. Eckel.

Illinois (Garry *et al.* 1990)—*Hypnum pratense;* and Connorsville interstadial deposits at Sefton Farm and the Cope Section, Fayette and Franklin counties, Indiana, respectively [the age of wood from the Connorsville interstadial is 20,000 ± 500 yr B.P. (I-610); Kapp and Gooding 1964, p. 311]—*Bryum lisae* var. *cuspidatum* (as *B. cuspidatum*), *Campylium polygamum, Ceratodon purpureus,* and *Rhizomnium punctatum* (as *M. punctatum*).

Three of the full-glacial mosses, *Cinclidium latifolium* (FIG. 3), *Didymodon asperifolius,* and *Drepanocladus brevifolius,* are of special interest in connection with the history of the arctic moss flora. The North American distribution of *C. latifolium* is shown in FIGURE 4, and Schofield (1972) has mapped North American occurrences of the other two species. All three mosses are cited by Steere (1965) as belonging to the circumpolar arctic element, and the main part of their contemporary ranges is the High Arctic. A fourth species, *Bryum neodamense* Itz. (FIG. 2) may also belong to this distribution type. In North America it is generally treated as a synonym of *B. pseudotriquetrum* (Hedw.) Gaertn., Meyer & Scherb. but is kept separate from it in the European floras of Nyholm (1958), Smith (1978), and others. Little attention has been paid to *B. neodamense* by North American bryologists, and the few published records of its occurrence are from Ellesmere Island (Holmen 1953; Brassard 1971, 1976), arctic Alaska (Steere 1978), Devon Island (Canadian Arctic Archipelago; Vitt 1975), and Yukon Territory and Quebec (Ireland *et al.* 1987). Its broad, obtuse, strongly concave, short-decurrent leaves seem diagnostic (FIG. 2). Moreover, the fossils are green-brown, unlike the largely black ones of *B. pseudotriquetrum,* which have lanceolate, sometimes broad, long-decurrent leaves, and which I have recovered repeatedly from Pleistocene sediments. If the status of *B. neodamense* as a species withstands taxonomic scrutiny, it may turn out to be frequent in North America in high latitude rich fens and other calcareous hydric habitats. It seems, however, to be absent in the continental rich fens of Alberta and nearby areas (D. H. Vitt, pers. comm., 2 Oct. 1989).

Midcontinent North America (ca. 40° North Latitude), based on the evidence presented here, may have served as a late-Pleistocene center of dispersal for elements of the arctic flora. For this to have happened, northward dispersal would have had to kept pace with deglaciation and outpaced postglacial climatic warming and the development of forest communities. There is some direct (fossil) evidence that populations of arctic mosses were present in younger deposits north of the full-glacial sites described here. For example, Janssens (1984) discovered fossils of *Cinclidium latifolium* and *Drepanocladus brevifolius* in late-glacial sediments deposited between 16,000 and 11,000 yr B.P. in Kotiranta Lake, Carlton County, northeastern Minnesota. Other late-glacial occurrences of arctic mosses north of the full-glacial sites described here are cited in Miller (1984). Moreover, it seems likely that a search of late-glacial sediments in lakes in southern and boreal Canada would reveal additional and younger fossils of arctic mosses. If this turns out not to be the case, populations of arctic species in midcontinent North America perhaps became extirpated as a result of climatic and other environmental changes and did not disperse northward, as has been postulated for the arctic beetles that occurred in the same region during the Wisconsinan glacial maximum (Schwert and Ashworth 1988). Extirpation or disperal as contrasting hypotheses can be evaluated as more data are gathered at new study sites in northern North America.

There is some evidence that high-arctic mosses were present at midlatitudes in North America earlier in the Pleistocene just before the onset of full-glacial conditions. Analyses of a buried organic bed exposed along Sixmile Creek, south of

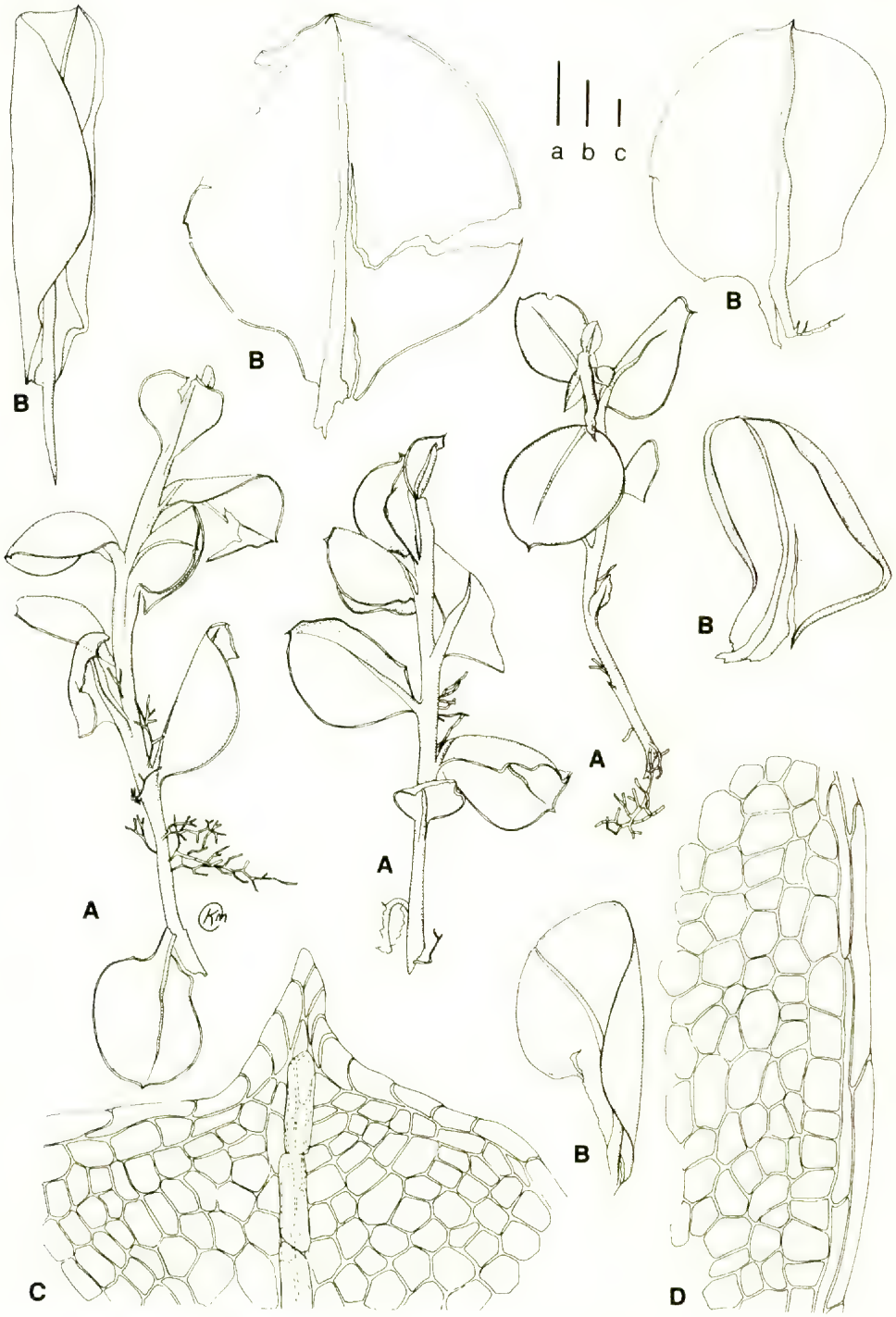


FIG. 3. Fossils of *Cinclidium latifolium* from the Clinton Power Station Site, De Witt Co., Illinois. A. Three plants (scale bar a). B. Five leaves from the same plant, note inrolled laminae in some leaves (b). C. Apex of leaf (c). D. Cells at edge of leaf (c). Scale bars: a = 1 mm, b = 0.5 mm, c = 10 μm. Drawings by Kathryn M. Conway.

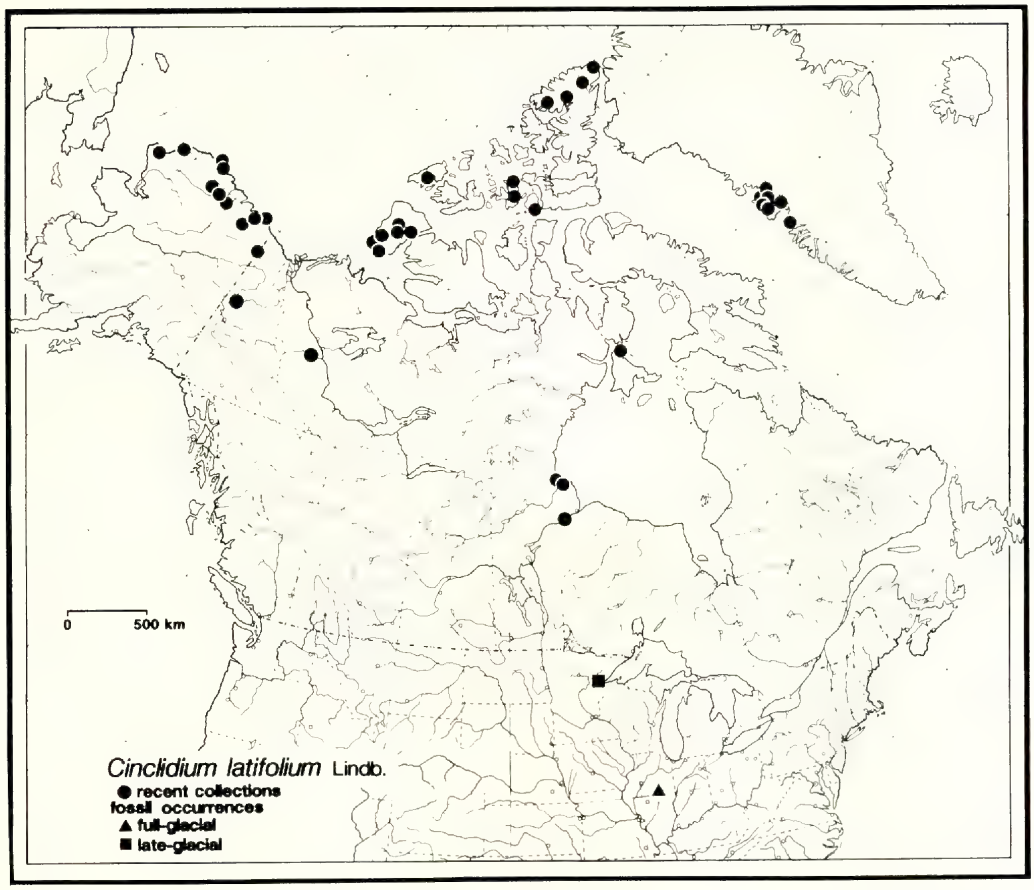


FIG. 4. Distribution of *Cinclidium latifolium* in North America. Map showing its present distribution and location of two late-Pleistocene fossil occurrences. Contemporary distribution based on map in Mogensen (1973), specimens examined, and information courtesy of G. S. Mogensen.

Ithaca, Tompkins County, New York (Miller and Schmidt, in prep.) produced abundant fossils of *Trichostomum arcticum*, a high-arctic species (Steere 1965; Schofield 1972), and other arctic-subarctic mosses, including *Hypnum bambergeri*, *Scorpidium turgescens*, *Timmia norvegica*, and at least 10 others. Leaves of the arctic-subarctic angiosperm *Dryas integrifolia* are abundant, and the pollen assemblage is dominated by sedge (77%), with pine (12%) and spruce (3%) subordinate. I have obtained the following AMS ages for two hardwood (*Salix?*) twigs from the organic bed: 27,000 ± 360 yr B.P. (Beta-27682, ETH-4474) and 33,940 ± 710 yr B.P. (Beta-32973, ETH-5699), indicating that the Sixmile Creek organic bed is 7,000 to 14,000 years older than the Illinois and Ohio full-glacial moss peats described here.

Current paleobotanical study in the North American Arctic has confirmed the antiquity of present members of the arctic flora such as *Cinclidium latifolium*, fossils of which are known from three Pliocene deposits, the Beaufort Formation of Prince Patrick and Meighen Islands and the Beaver Peat, west-central Ellesmere Island (Matthews and Ovenden 1990). Arctic mosses are also present in Plio-Pleistocene peats of Kap København, North Greenland (Mogensen 1984). These late Tertiary–early Quaternary paleobryofloras contain the remains of numerous mosses. The age of the Beaufort Formation on Meighen Island is ca. 3 Ma (million years) on the basis of geological and paleontological evidence (Matthews and

Ovenden 1990), while that of the Kap København formation is younger, 2.5–2.0 Ma (Bennike 1990). Scattered trees, *Picea mariana, Thuja occidentalis,* and *Larix groenlandii* (extinct), grew in places surrounded by open tundra vegetation in North Greenland at this time (Bennike and Böcher 1990), whereas the older (and more northern) Beaufort peats of Meighen Island contain spruce and pine macroremains together with fossils of tundra plants (Matthews and Ovenden 1990). It is possible that these late-Tertiary floras minus the trees, many of the shrubs, and the extinct species, would have been similar floristically to contemporary Arctic floras. Thus, many moss species of current arctic distribution have had a history of occurrence at high latitudes over millions of years.

The traditional interpretation has held that the present arctic flora assembled after the end of the Pleistocene through dispersal from unglaciated refugia in Beringia and parts of arctic and boreal Canada (Steere 1965). To this may now be added dispersal northward from areas just beyond or near the limit reached by the continental ice margin in central North America. The fate of populations of arctic species of mosses known to have occurred at low elevation in an area about 1000 km from east to west at the time the ice margin reached its maximum late-Wisconsinan extent, or some several thousands of years before this, will be discovered during studies of moss-rich sediments in the region between 40° North Latitude and the Arctic. Because fossils of arctic mosses have been found in younger sediments at places 750 km north of the midcontinent area (ca. 47° North), additional information should allow the role of a southern center of dispersal to be understood more fully.

ACKNOWLEDGMENTS

I thank the following individuals for access to deposits they discovered or for providing samples or information: L. R. Follmer, S. T. Jackson, J. E. King, T. V. Lowell, G. S. Mogensen, K. M. Savage, V. E. Schmidt, and J. A. Snider. I am also grateful for comments on a draft of the manuscript from C. A. Chumbley.

This paper is published as contribution number 706 of the New York State Science Service.

LITERATURE CITED

Baker, R. G., R. S. Rhodes II, D. P. Schwert, A. C. Ashworth, T. J. Frest, G. R. Hallberg and J. A. Janssens. 1986. A full-glacial biota from southeastern Iowa, USA. J. Quaternary Sci. 1: 91–107.

———, A. E. Sullivan, G. R. Hallberg and D.G. Horton, 1989. Vegetational changes in western Illinois during the onset of late Wisconsinan glaciation. Ecology 70: 1363–1376.

Bennike, O. 1990. The Kap København Formation: Stratigraphy and paleobotany of a Plio-Pleistocene sequence in Peary Land, North Greenland. Meddel. Grønland, Geosci. 23: 1–85 + 1 unpaged table.

——— and J. Böcher. 1990. Forest-tundra neighboring the North Pole: Plant and insect remains from the Plio-Pleistocene Kap København Formation, North Greenland. Arctic 43: 331–338.

Brassard, G. R. 1971. The mosses of northern Ellesmere Island, arctic Canada. II. Annotated list of the taxa. Bryologist 74: 282–311.

———. 1976. The mosses of northern Ellesmere Island, arctic Canada. III. New or additional records. Bryologist 79: 480–487.

Burns, G. W. 1958. Wisconsin age forests in western Ohio II. Vegetation and burial conditions. Ohio J. Sci. 58: 220–230.

Crum, H. 1972. The geographic origins of the mosses of North America's eastern deciduous forest. J. Hattori Bot. Lab. 35: 269–298.

Garry, C. E., D. P. Schwert, R. G. Baker, T. J, Kemmis, D. G. Horton and A. E. Sullivan. 1990. Plant and insect remains from the Wisconsinan interstadial/stadial transition at Wedron, north-central Illinois. Quaternary Res. 33: 387–399.

Goldthwait, R. P. 1958. Wisconsin age forests in western Ohio I. Age and glacial events. Ohio J. Sci. 58: 209–219.

Holmen, K. 1953. Bryophytes of Fosheim Pennisula, Ellesmere Island. Bryologist 56: 242–248.

Ireland, R. R., G. R. Brassard, W. B. Schofield and D. H. Vitt. 1987. Checklist of the mosses of Canada II. Lindbergia 13: 1–62.

Janssens, J. A. 1984. *Cinclidium latifolium* Lindb. in the late-glacial of northern Minnesota, USA. Lindbergia 10: 121, 122.

———. 1990. Bryophytes. *In:* B. G. Warner (ed.), *Methods in Quaternary Ecology.* Geoscience Canada Reprint Series 5: 23–36.

——— and R. G. Baker. 1984. A full-glacial bryophyte assemblage from southeastern Iowa, USA. J. Bryol. 13: 201–207.

Kapp, R. O. and A. M. Gooding. 1964. Pleistocene vegetational studies in the Whitewater Basin, southeastern Indiana. J. Geol. 73: 307–326.

King, F. B. 1979. Plant macrofossils from the Athens North Quarry. Illinois State Geol. Surv. Guidebook 13: 114, 115.

King, J. E. 1979. Pollen analysis of some Farmdalian and Woodfordian deposits, central Illinois. Illinois State Geol. Surv. Guidebook 13: 109–113.

Lowell, T., K. Savage, A. Dell, A. V. Morgan, J. Pilney, N. Miller and L. Shane. 1990a. Late Wisconsin glacial maximum biota, Cincinnati, Ohio. Canad. Quaternary Assoc. Amer. Quaternary Assoc. First Joint Meeting Program Abstr. Page 23. [Quaternary Sci. Inst., Univ. Waterloo, Canada.]

———, ———, C. S. Brockman and R. Stuckenrath. 1990b. Radiocarbon analyses from Cincinnati, Ohio, and their implications for glacial stratigraphic interpretations. Quaternary Res. 34: 1–11.

Martin, P. S. 1959. How many logs make a forest? Ohio J. Sci. 59: 221, 222.

Matthews, J. V., Jr. and L. E. Ovenden. 1990. Late Tertiary plant macrofossils from localities in arctic/subarctic North America: A review of the data. Arctic 43: 364–392.

Miller, N. G. 1976. Quaternary fossil bryophytes in North America: A synopsis of the record and some phytogeographic implications. J. Hattori Bot. Lab. 41: 73–85.

———. 1979. Paleoecological comments on fossil mosses in a buried organic bed near Peoria, Tazewell County, Illinois. Illinois State Geol. Surv. Guidebook 13: 116.

———. 1984. Tertiary and Quaternary fossils. *In:* R. M. Schuster (ed.), *New Manual of Bryology* 2: 1194–1232. Nichinan, Japan: Hattori Botanical Laboratory.

———. 1990. Plant macrofossils. *In:* A. V. Morgan (ed.), *Biological Techniques in Paleoenvironmental Interpretation.* Pages 30–72. Quaternary Sciences Institute. University of Waterloo. Waterloo, Ontario.

——— and S. T. Jackson. 1989. The setting and composition of full-glacial moss floras in the American Middle West. Am. J. Bot. 76(6): 12. [Abstract.]

Mogensen, G. S. 1973. A revision of the moss genus *Cinclidium* Sw. (Mniaceae Mitt.) Lindbergia 2: 49–80.

———. 1984. Pliocene or early Pleistocene mosses from Kap København, North Greenland. Lindbergia 10: 19–26.

Montagnes, R. J. S. 1990. The habitat and distribution of *Meesia triquetra* in North America and Greenland. Bryologist 93: 349–352.

Nyholm, E. 1954–1969. *Illustrated Moss Flora of Fennoscandia* II. Musci. Lund: CWK Gleerup.

Schofield, W. B. 1969. Phytogeography of northwestern North America: Bryophytes and vascular plants. Madroño 20: 155–207.

———. 1972. Bryology in arctic and boreal North America and Greenland. Canad. J. Bot. 50: 1111–1133.

——— and H. A. Crum. 1972. Disjunctions in bryophytes. Ann. Missouri Bot. Gard. 59: 174–202.

Schuster, R. M. 1983. Phytogeography of the Bryophyta. *In:* R. M. Schuster (ed.). *New Manual of Bryology* 1: 463 -626. Nichinan, Japan: Hattori Botanical Laboratory.

Schwert, D. P. and A. C. Ashworth. 1988. Late Quaternary history of the northern beetle fauna of North America: A synthesis of fossil and distributional evidence. Mem. Entomol. Soc. Canada 144: 93–108.

Smith, A. J. E. 1978. *The Moss Flora of Britain and Ireland.* Cambridge and other cities: Cambridge University Press.

Steere, W. C. 1953. On the geographical distribution of arctic bryophytes. Publ. Stanford Univ. Biol. Sci. 11: 30–47.

———. 1965. The boreal bryophyte flora as affected by Quaternary glaciation. *In:* H. E. Wright, Jr. and D. G. Frey (eds.), *The Quaternary of the United States.* Pages 485–495. Princeton, New Jersey: Princeton University Press.

———. 1969. Asiatic elements in the bryophyte flora of western North America. Bryologist 72: 507–512.

———. 1978. The mosses of arctic Alaska. Bryophyt. Biblioth. 14: i–x, 1–508.

Vitt, D. H. 1975. A key and annotated synopsis of the mosses of the northern lowlands of Devon Island, N.W.T., Canada. Canad. J. Bot. 53: 2158–2197.

Wright, H. E., Jr. 1981. Vegetation east of the Rocky Mountains 18,000 years ago. Quaternary Res. 15: 113–125.

Contr. Univ. Mich. Herb. 18:87–90. 1992.

HYPNUM PLICATULUM IN EASTERN NORTH AMERICA

W. B. Schofield
Department of Botany
University of British Columbia
Vancouver, B.C., Canada V6T 2B1

Hypnum plicatulum (Lindb.) Jaeg. was reported first from North America by Lindberg (1903) under the name *Stereodon plicatulus* Lindb. The specimen on which this record is based came from Lake Lindeman in northern British Columbia where it was collected by R.S. Williams. Lindberg provided figures that point out its distinctions from *H. callichroum* Brid.

Crum and Anderson (1981) noted, among the excluded species of Hypnaceae, the name *H. molluscoides* Kindb., a species described from Newfoundland, but in which the type specimen, characteristic of many of Kindberg's new species described from Canada, is difficult to locate with confidence. Dr. H. Ando (*in litt.*, 1992) has stated that he has seen several specimens from Newfoundland and Labrador that bear locality, dates and collectors cited by Kindberg and labelled as *H. molluscoides* Kindb. These are housed in diverse European herbaria (BM, PC, etc.) All are *H. plicatulum*. Thus Ando's (1972) conclusion that *H. molluscoides* is synomymous with *H. plicatulum* is confirmed.

Grout (1932) first noted *H. plicatulum* from eastern North America under the name *H. subplicatile* (Lindb.) Limpr. His report was very tentative and based on a specimen from Seal Island, Labrador described as *Hypnum implexum* Ren. & Card. that he noted to match the specimens of the Lake Lindeman plants reported by Lindberg. Ando (*in litt.*, 1992) noted that he had examined this specimen and concluded it to be identical to *H. plicatulum*. The report of Tuomikoski *et al.* (1973) of *H. plicatulum* from Newfoundland carried the same uncertainty.

It can be noted here that there is unquestionable *H. plicatulum* in eastern North America. It is best represented in the Gulf of St. Lawrence region, and is especially frequent on calcareous substrata in the Mingan Islands, Quebec, and relatively frequent in Nova Scotia, especially on the south shore of the Bay of Fundy on North Mountain, and in the Cape Breton Highlands.

Hypnum plicatulum belongs to the troublesome section *Hamulosa* B.S.G. as emended by Ando (1973b). Besides *H. hamulosum* B.S.G. as the type of the section, it includes *H. plicatulum, H. callichroum, H. subimponens* Lesq., *H. emodi-fertile* Ando, *H. aemulans* Breidl. *in* Limpr., and possibly an undescribed species from arctic and subarctic regions.

Although *H. plicatulum* shows some variability in growth form and color, related in large part to insolation and humidity of its environment, it usually can be distinguished from related species. Persson (1947) pointed out the main distinguishing characters. From *H. callichroum* and *H. hamulosum* it can be distinguished by its nearly auriculate leaves that possess a small alar cluster of cells displaced well away from the auriculate area and close to the stem. In *H. callichroum,* where an auriculate portion is present, it is formed of a well-differentiated cluster of thinner-walled and enlarged cells. Ando (*in litt.*, 1992) noted that the sporangium is plicate when dry, a feature not shared by related species. Neither *H. hamulosum* nor *H.*

subimponens exhibits the auriculate region, but the leaf margins curve gradually to the insertion. *Hypnum emodi-fertile*, among other features, possesses rather short acuminate leaves, and the alar cells form a conspicuous group (Ando, 1973a). *Hypnum aemulans*, according to Ando (1972), shows well-developed hyaline alar cells and thus resembles *H. callichroum* rather than *H. plicatulum*.

Although Ando (1972) shows a broken distribution for *H. plicatulum* in North America, it appears that the species ranges across the boreal portion of Canada. The unsatisfactory bryological exploration of much of that region probably explains the gap in distribution (Fig. 1).

Hypnum fertile Sendtn. has been sometimes mistaken in North America for *H. plicatulum*. It is possible that I have perpetuated this error in my M.A. thesis (Schofield, 1956), where I failed to recognize *H. plicatulum* as a distinct species and combined it with *H. callichroum*. Furthermore, I confused *H. plicatulum* specimens of eastern North America with *H. fertile*. As Ando (1973) has noted, the stems of section *Fertilia* are not strictly hyalodermous, although the epidermal cells are sometimes somewhat thin-walled on the outer surfaces. Stem leaves in *Fertilia* have thin-walled hyaline cells in an excavate group toward the leaf base. This latter character is absent in the section *Hamulosa*. Furthermore, *H. fertile*, an autoicous species, usually has sporophytes, while the *Hamulosa* frequently lack them. The North American range of *H. fertile* is unsatisfactorily understood, but it is clearly confined to eastern North America, and the range overlaps with *H. plicatulum* in Nova Scotia, at least.

Since a complete description is difficult to find, one is provided, based on North American specimens:

Plants soft, forming creeping mats or turfs of suberect interwoven shoots, with stems 2–5 cm long and bearing regular or irregular branches 0.2–0.5 cm long, yellowish- to golden-green, when best developed, closely and regularly pinnate. Stems green to yellowish or occasionally with a tinge of brown, cortical cells hyalodermous, inner cells incrassate; pseudoparaphyllia foliose, often forked, with attenuate uniseriate tips on the lobes. Stem leaves curved to falcate-secund, 1.0–1.5 mm long, ovate lanceolate to narrowly triangular, inserted with an auriculate base and curving gradually to a long attenuate apex; margin often toothed on auriculate portion, entire or toothed in upper portion, plane; costa short and double or inconspicuous; cells linear flexuose, 50(–60)–70(–80) μm long; alar cells 5–6, angular, often colored, triangular to rectangular or rhomboidal, 6–15 μm long, thick-walled except for the outermost and lowermost one, abruptly different from the stem cortical cells and rest of the leaf cells, sometimes reduced or absent. Setae red, 2.0–2.3 cm long, smooth; sporangia 1.5–2.0 mm long, curved, somewhat contracted below mouth and plicate when dry; operculum conic, 0.5 mm long; exostome teeth yellow to brownish.

Habitat—Growing up tree bases, on logs, over humus on cliff shelves or on humus over boulders, forest floor to bog margins, most frequently in somewhat shaded sites, especially on slopes below cliffs.

Distribution—A predominantly boreal species: in eastern North America known from Nova Scotia, New Brunswick, Newfoundland, Labrador, Quebec, Baffin Island, and Ontario. Apparently rare in the Arctic Archipelago, also in western North America: Manitoba, MacKenzie District, N.W.T., Yukon, Alaska, and northern British Columbia.

Representative specimens examined: Greenland. Narssaq, on Sarssagsund at Grønlands Geologiske Undersøgelset camp, *Steere 62-1046* (CANM). Canada. Manitoba: Fort Hall Lake, *Scotter 3493*

FIG. 1. Canadian and Alaskan distribution of *Hypnum plicatulum*.

(UBC). Newfoundland: Benoit's River, Humber Arm, Humber, *Tuomikoski 5371* (CANM); Flower's Cove, St. Barbe, *Tuomikoski 4246* (CANM); Gros Morne National Park, Western Brook Pond, *Vitt 31344* (ALTA). Northwest Terrritories: Baffin Is., Cumberland Sound, vicinity of Pangnirtung, *Wynne-Edwards 28* (CANM). Nova Scotia: Pictou Co., Brookland, *Schofield, Belland & Weber 89746* (UBC);

Kings Co., Cambridge, *Schofield 2785* (UBC); Lunenburg Co., Deep Cove, *Ireland 17669* (UBC); Digby Co., Long Island, Flower's Cove, *Schofield & Schofield 95539* (UBC). Ontario: Lake Nipigon, SW corner of Ellis Island, *Garton 21930* (CANM). Quebec: Cap Chat, *Fabius 4990* (CANM); Ungava Bay, Fort Chimo, *Lepage 13689* (UBC); Great Whale River, *Tuomikoski 4901* (CANM); Lac Guillaume-Delisle, Richmond Gulf, *Ireland 21427* (CANM); Mingan Archipelago, Grosse Île au Marteau, *Hedderson 7684* (UBC), Île du Havre, *Schofield, Belland & Hedderson 93459* (UBC), Île de Fantôme, *Schofield, Belland & Hedderson 94140* (UBC), Île Ste. Geneviéve, *Schofield, Belland & Hedderson 94337* (UBC).

ACKNOWLEDGMENTS

For loan of specimens, I thank R. R. Ireland (CANM) and D. H. Vitt (ALTA). Dr. R. J. Belland has offered comments on the manuscript. Research has been supported by the Natural Sciences and Engineering Research Council of Canada. Research on *Hypnum* was begun in 1956 under the direction of the late W. C. Steere. I profited also from correspondence with the late H. Persson (Stockholm) and especially with H. Ando (Hiroshima), whose knowledge of the genus is unsurpassed.

LITERATURE CITED

Ando, H. 1972. Distribution and speciation in the genus *Hypnum* in the circum-Pacific region. J. Hattori Bot. Lab. 35: 68–98.

———. 1973a. Miscellanea bryologica Asiae orientalis III. Hikobia 6: 203–216.

———. 1973b. Studies on the genus *Hypnum* Hedw. II. J. Sci. Hiroshima Univ., Ser. B., Div. 2 (Bot.), 14: 165–207.

Crum, H. A. and L. E. Anderson. 1981. Hypnaceae. Excluded. *In: Mosses of eastern North America* 2: 1206, 1208. Columbia University Press, New York.

Grout, A. J. 1932. *Hypnum subplicatile. In: Moss flora of North America north of Mexico* 3(3): 128. Privately published by the author, Newfane, Vermont.

Lindberg, H. 1903. *Stereodon plicatulus* Lindb. Bryologist 6: 82, 83.

Persson, H. 1947. Further studies on Alaskan-Yukon bryophytes. Bryologist 50: 279–310.

Schofield, W. B. 1956. *The relationships and geographic distribution of Canadian and Alaskan species of Hypnum.* M. A. Thesis, Stanford University.

Tuomikoski, R., T. Koponen and T. Ahti. 1973. The mosses of the island of Newfoundland. Ann. Bot. Fennici 10: 217–264.

Contr. Univ. Mich. Herb. 18:91–97. 1992.

OBSERVATIONS ON SPHAGNUM FITZGERALDII

Lewis E. Anderson
Department of Botany
Duke University
Durham, NC 27706, U.S.A.

Sphagnum fitzgeraldii Ren. & Card. is an infrequent peat moss, endemic to the southeastern Coastal Plain of the United States. It belongs to Section *Cuspidata* and bears resemblances to *S. cuspidatum* Ehrh. *ex* Hoffm., *S. trinitense* C. Müll. and *S. torreyanum* Sull. Little has been written about its biology, especially its ecology, phenology, distribution, and cytology. Some of these features are unique to the species and are not generally appreciated. I have had extensive field experience with *S. fitzgeraldii* extending over a period of more than thirty years, during which I have accumulated considerable information about it. This paper summarizes these observations.

It was my pleasure to introduce Howard Crum to this species on one of our many field excursions to the southeastern Coastal Plain and to discuss with him many of the singularities. It is highly appropriate, therefore, to dedicate this contribution to him.

TAXONOMY

Sphagnum fitzgeraldii is distinguished from its closest relatives by relatively short, ovate to oblong-elliptic branch leaves with the margins serrulate almost to the leaf bases by projecting cell ends. (The serrulations are not due to resorption of a portion of the border cells of the branch leaves, as in many *Sphagna*). Furthermore, the branch leaf apices, excepting those at the tips of the branches, are broadly truncate, generally with five or more teeth across the leaf apices. The ends of branches often end in a cluster of leaves with narrowly elongate apices, as in the three closest relatives listed above. Most of the confusion between *S. fitzgeraldii* and *S. trinitense,* both of which have serrulate branch leaf margins, seems to be due to a misreading of this character. The branch leaves of *S. cuspidatum* and *S. torreyanum* are entire, although some taxonomists allow slight serrulations at the very tips of the longer leaves at the ends of branches (e.g., Crum 1984).

Plants of *S. fitzgeraldii* are uniformly hemi-isophyllous. The stem leaves are mostly larger than the branch leaves, very concave, and entire-margined, except at the rounded apex. Like the branch leaves, they are also fibrillose and porose to the base.

The hyaline cells of the branch leaves have small ringed or unringed pores on both surfaces, often confined to the cell ends and occurring in threes at adjacent cell-angles. Some of the pores are faint and difficult to demonstrate without heavy staining.

Plants of *S. fitzgeraldii* are mostly smaller than those of its relatives and are lax and soft, especially when dry. A distinctive character is that the branches toward the tip of the capitulum end in prominent buds, which, in dried plants, are pointed and especially noticeable. This character is especially useful in field recognition if the truncate leaf tips cannot be seen.

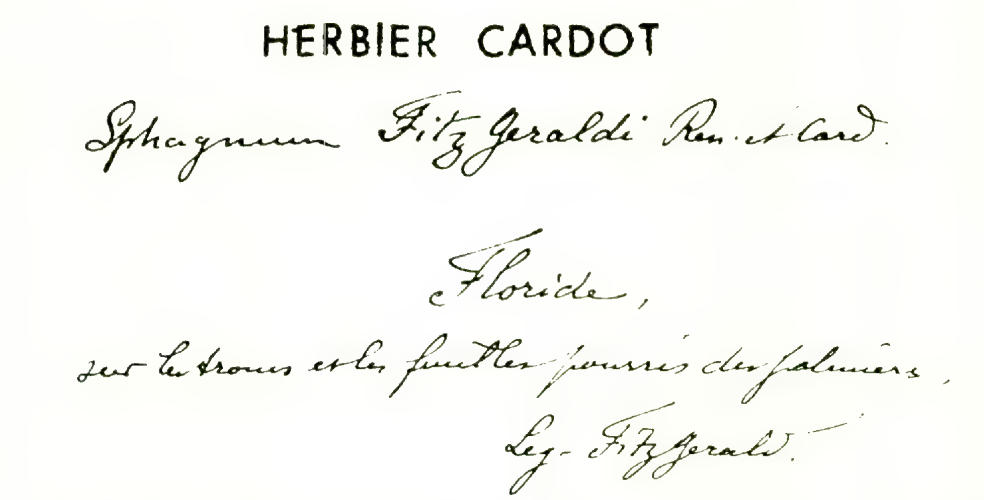

HERBIER CARDOT
Sphagnum Fitz Geraldi Ren. et Card.
Floride,
sur les troncs et les feuilles pourries des palmiers,
Leg. Fitz Gerald.

FIG. 1. Copy of herbarium label from one of the three type collections of *Sphagnum fitzgeraldii* in PC.

The first published description of *S. fitzgeraldii* was attributed to Renauld ("*in litt.*") in the Lesquereux and James *Manual* (1884). The protologue is obviously a condensed translation of a description published a year later by Renauld and Cardot (1885), in which the citation reads, "*Sphagnum Fitzgeraldi* Ren. et. Card. Spc. nov. Lesquereux Manual, N. Am., p. 23." The type comprises three packets in the Cardot Herbarium (PC), one of which needs to be selected as the lectotype. I intend to do this as soon as I am able to examine the three specimens. They are obviously all from the same collection and each of the three labels specify "Ren. & Card." as authors of the "Spec. Nov." Through the courtesy of Dr. Hélène Bischler, a facsimile of one of the labels from the Cardot Herbarium is shown in FIG. 1. Clearly, Cardot was involved in studying and describing the new species. The omission of his name in the Lesquereux and James *Manual* is an error which has been passed along by Andrews (1913, 1940), Crum *et al.* (1965, 1973), Crum (1984), and Anderson (1990), among others. *Index Muscorum* (van der Wijk, *et al.* 1967) cited "Ren. & Card.," which, in my opinion, is the correct interpretation.

Renauld and Cardot (1885) incorrectly placed *S. fitzgeraldii* in Section *Hemitheca,* which Lindberg (Braithwaite 1878) erected for the single species, *S. pylaesii* Brid. Renauld and Cardot were misled, apparently, by the single collection of Fitzgerald's from Florida, the plants of which are mostly monopodial or forked (". . . ses rameaux solitares ou géminés . . ."). The type collection very likely consisted mainly of juvenile plants regenerated from desiccated plants that had not yet produced capitula. According to the label (FIG. 1), the habitat was rotten leaves and stems of palms. Although not stated, most likely the regenerating plants came from a shallow depression (possibly in a hammock, based on the presence of palms) which had previously dried up.

Warnstorf (1911) clarified the relationship of *S. fitzgeraldii* by treating it as a variety of *S. trinitense,* which was a curious bit of conservatism from a renowned splitter. To compensate for this lapse, however, he described *Sphagnum trinitense f. immersum* and *S. mohrianum,* both of which are synonyms of *S. fitzgeraldii,* as Crum (1984) has pointed out. I should add that Crum prefers to treat *S. trinitense* as *S. cuspidatum* var. *serrulatum* (Schlieph.) Schlieph.

DISTRIBUTION

Sphagnum fitzgeraldii is restricted to central and northern Florida and a narrow strip of land near the ocean, extending along the Gulf of Mexico, from Jackson County, Mississippi, Alabama, the panhandle of Florida, Georgia, South Carolina, and north to Craven and Pamlico counties, North Carolina (FIG. 2). Why its range ends so abruptly here is puzzling. Repeated searches by many knowledgeable collectors, including Norton Miller, Howard Crum, Richard Andrus, Wolfgang Maass, Eric Karlin, and myself, in the northern coastal counties of North Carolina and southeastern Virginia have been unsuccessful in extending its range beyond that shown in the map (FIG. 2).

Crum (1984) reported *S. fitzgeraldii* from Santa Cruz, Gálapagos Islands, based on a specimen collected by D. Hunt, December 17, 1973, "Bellavista, on path to

FIG. 2. Map, showing the known distribution of *Sphagnum fitzgeraldii*.

summit of crater" (MICH). The specimen was originally identified as *S. cuspidatum* var. *serratum* (= *S. trinitense*) by A. LeRoy Andrews and later annotated by Howard Crum as *S. fitzgeraldii*. Through the courtesy of the latter, I have examined it recently and, I, too, find it puzzling. The plants have the soft texture of *S. fitzgeraldii* and the branch leaves are serrulate and somewhat truncate, but much less so than in *S. fitzgeraldii*. Also, the branch leaves are more straight-sided and much less ovate than in *S. fitzgeraldii*. The chlorophyllose cells of the branch leaves of the Gálapagos specimen are triangular in section, barely exposed on the upper surface; in contrast, these cells are trapezoidal to rectangular in section in *S. fitzgeraldii*.

At my request, Crum recently reexamined the Gálapagos specimen, and he now agrees that it is not that species (personal communication). The specimen is somewhat sparse and scrappy and neither of us is willing to assign a name to it. Possibly, it is an undescribed species, but better material is required before it can be dealt with satisfactorily.

ECOLOGY

Sphagnum fitzgeraldii occurs submerged or barely emergent in shallow pools, ditches, and other depressions that dry out completely for two or more months during the annual summer droughts characteristic of the southern United States. It may be found at the fluctuating margins of permanent water. Such margins are dry for most of the summer.

Sphagnum fitzgeraldii is principally a moss of disturbances; its habitats are strongly influenced by successional forces, principally fire and human activities. The vegetation of the southeastern Coastal Plain for a very long time has been shaped almost entirely by fire. Nearly all the native plants have a degree of fire resistance. Pines dominate because they are more resistant to fire than are hardwoods. Repeated fires kill back the hardwood seedlings and shrub understory. Succession is interrupted and pines continue to dominate, although fire keeps them thinned and spaced, opening up the canopy. In pine flatwoods where the winter water table is high enough, shallow depressions fill with water and provide suitable habitats for *S. fitzgeraldii*.

Pocosins are evergreen shrub bogs overtopped by scattered pocosin or pond pine (*Pinus serotina* Michx.). It is the only pine that can tolerate the high water table for long periods. It is also exceptionally resistant to fire. Even if the trunk is killed, numerous sucker shoots will emerge from the base. The understory consists of a thick, impenetrable tangle of evergreen shrubs, small trees, and vines. Unless there are openings, the interior of pocosins is too dense to permit much development of *Sphagna*. Fire and other disturbances, however, may open up enough space for the development of a genuine peat bog, although such bogs are not suitable habitats for *S. fitzgeraldii*, which apparently is unable to compete with more aggressive species.

The ecotone between pine flatwoods and pocosins is called savannah, which is composed of scattered, well-spaced pines, generally long-leaf (*P. palustris* Miller), slash (*P. elliottii* Engelm.), or, rarely, loblolly (*P. taeda* L.). Thus, a savannah always adjoins or encircles a pocosin. The ecotone between the two, especially the wetter side toward the pocosin, is a prime habitat for *S. fitzgeraldii*. It is often found at the shallow ends of roadside ditches through or along the margins of pocosins.

Even the smallest depressions can support this moss if they retain water during the winter growth period. I have collected it in deer tracks, as well as in human boot tracks in wet savannahs.

More or less open hardwood swamps also provide habitats. They are generally flooded during the winter months and dry in summer. I have seen a number of specimens from swamps from the panhandle of Florida, and farther south, in peninsular Florida, I have collected it from hammocks, which are small islands of more or less tropical vegetation surrounded by wetlands.

Several collections have been made from wet seeps, usually in sandy soil that dries up in summer. This type of habitat is not uncommon along some of the rolling sand ridges in the panhandle of Florida. On occasion I have observed thin, delicate sheets of *S. fitzgeraldii* along these seep lines.

PHENOLOGY

Most of the phenological information presented here was obtained from a single large colony of *S. fitzgeraldii* that Norton Miller and I discovered independently in Brunswick County, North Carolina, in 1973. It was the largest colony of this species that either of us has ever encountered. When we first observed this colony, the habitat was a shallow pool, scarcely more than 16 cm deep, but nearly 100 m long and from 10 to 15 m wide, created by soil removal for road maintenance. When first discovered, in February, the pool was almost completely filled with fruiting *S. fitzgeraldii*. Located in the ecotone between a wet savannah and a pocosin, the habitat was artificially maintained by a hunting club that kept vegetation cut back to foster quail populations. I have kept the site under observation until the present time.

Unfortunately, in the early 1980's, the club abandoned the site for hunting, and maintenance of the site ceased. Since then, the site has not burned, and invasion by pines (*Pinus serotina* Michx.), woody shrubs, and tall herbs have gradually replaced the moss. Succession in such areas is swift and, by the summer of 1991, *S. fitzgeraldii* had almost disappeared, presumably because of shading and competition from vascular plants. Only a few sparse clumps remained at that time.

Essentially all the vegetative growth in *S. fitzgeraldii* occurs in the winter and spring months when the shallow pools in which it grows are filled with water. In late May and June rainfall decreases, temperatures rise, evaporation increases and the shallow winter pools that support the moss gradually dry up. By mid-summer, most of the pools that support it are completely dry. If the summer drought is severe, the moss bleaches into relatively thin sheets and appears lifeless.

With the onset of late fall and winter rains, however, many of these seemingly lifeless plants regenerate from the younger stems and produce new plants directly, without forming protonemata. The new shoots are monopodial at first, but soon develop capitula, and by December, the new shoots are capable of producing sex organs. I have observed mature antheridia as early as December 15, and as late as February 2. Although, I have not been able to locate unfertilized archegonia, I have observed barely swollen capsules in late December and early January.

The earliest meiotic capsules I have observed were collected on February 2; the latest were taken on March 12. *Sphagnum fitzgeraldii* is dioicous and, as might be expected, it is not often found in fruit. During the approximately 10-year period

that the Brunswick County colony flourished, I found abundant capsules during seven of those years. In 1979 and 1980 only a few capsules were noticed. The largest crop of capsules occurred in 1981. During the successional period, beginning in 1982, when the colony began to diminish, capsule production was sparse and erratic, and I observed no capsules at this site after 1987.

Although, generally, plants of *S. fitzgeraldii* become heavily stressed during the summer droughts and regenerate when the shallow pools recharge with water in the fall months, I have observed colonies in Florida and North Carolina in which, apparently, plants were not stressed sufficiently during the summer to require regeneration. Growth continued terminally from shoots of the previous year by the usual forking procedure.

CYTOLOGY

The chromosome number of *S. fitzgeraldii* has not been published previously. Using essentially standard squash techniques (Anderson and Bryan 1987), the chromosome number, $n = 19 + 2m$, was established for the population discussed above (Shallow pool in an open, wet savannah, adjacent to a pocosin, 9.7 miles southeast of Supply, NC on Highway 211, Brunswick County, North Carolina; February 15, 1976; voucher, DUKE).

All species of *Sphagnum* thus far investigated have 19 or 39 bivalents at meiosis. In addition, a variable number of tiny, faintly staining *m*-chromosomes have been reported for various species (Fritsch 1982). In addition to the 19 regular bivalents observed in *S. fitzgeraldii*, two very faintly stained *m*-chromosomes are present. In most spore mother cells, the *m*'s are exceedingly difficult to distinguish (Fig. 3, for instance), but by intensive staining and careful squashing, they can be demonstrated (Figs. 4, 5). They are in Fig. 4 near the center of the metaphase plate, which has been spread out by squashing. One of the *m*-bivalents (to the right) has already disjoined into half-bivalents. In Fig. 5, the square-like configuration in the center consists of two sister chromatids to the right and a half-bivalent to the left not yet divided into sister chromatids. This precocious behavior indicates that they are probably achiasmate. Bryan (1955) has described the meiotic behavior of *m*-chromosomes in other species of *Sphagnum*. Their significance, if any, is still unknown.

FIGS. 3–5. Meiotic chromosomes of *Sphagnum fitzgeraldii*, × 3430. 3. Prometaphase, showing 19 bivalents. *M*-chromosomes are not stained. 4. Heavily stained early metaphase, showing, at the center, one *m*-bivalent and two disjoined *m*-half-bivalents. 5. Similar, except the *m*-bivalent toward the center has disjoined into a half-bivalent and two half-chromatids; the second *m*-bivalent below has disjoined into two half-bivalents.

DISCUSSION

It is apparent that the life history and ecology of *S. fitzgeraldii* are meshed. Its growth and reproduction occur during the wet winter months when the small pools in which it grows are filled with water. Its ability to withstand extreme desiccation and to recover relatively quickly through direct regeneration without going through a time-consuming protonematal stage enables it to occupy habitats that dry out for long periods during the summer. It is largely restricted to these habitats because it manifestly cannot compete successfully with *S. cuspidatum* and *S. trinitense* in pools and ditches in which water is more or less permanent, or at least is not dry for long periods.

The rarity of *S. fitzgeraldii* is doubtless related to its narrow habitat restriction. It is unable to compete successfully with *S. cuspidatum, S. trinitense, S. torreyanum,* and the two varieties of *S. macrophyllum* Brid. in permanent water habitats. Its life history and its resistance to desiccation enables it to survive in shallow and more or less temporary depressions, pools, ditches, etc., Such habitats are easily altered by successional shifts so that its existence is usually precarious. Human disturbances, such as roadside ditches, and telephone and electric transmission lines through and alongside wetlands, have provided additional habitats. On the other hand, extensive drainage operations are drastically reducing habitats by severely lowering water tables in many areas where *S. fitzgeraldii* might grow. It is not by any means an endangered species, but, like other wetland species, there is a threat hanging over it.

LITERATURE CITED

Anderson, L. E. 1990. A checklist of *Sphagnum* in North America north of Mexico. Bryologist 93: 500, 501.

——— and V. S. Bryan. 1987. M-chromosome behavior in the moss, *Clasmatodon parvulus*. Mem. New York Bot. Gard. 45: 122–134.

Andrews, A. L. 1913. Sphagnales. N. Amer. Fl. 15: 1–31.

———. 1940. List of North American species of *Sphagnum*. Bryologist 43: 132.

Braithwaite, R. 1878. *The Sphagnaceae or peat mosses of Europe and North America*. Hardwicke & Bogue, London. 91 pp. + XXIX pls.

Bryan, V. S. 1955. Chromosome studies in the genus *Sphagnum*. Bryologist 58: 16–39.

Crum, H. 1984. Sphagnopsida. Sphagnaceae. N. Amer. Fl. II, 11: 1–180.

———, W. C. Steere and L. E. Anderson. 1965. A list of the mosses of North America. Bryologist 68: 377–432.

———, ——— and ———. 1973. A new list of mosses of North America north of Mexico. Bryologist 76: 85–130.

Fritsch, R. 1982. Index to plant chromosome numbers—Bryophyta. Regnum Veg. 108: 1–268.

Lesquereux, L. and T. P. James. 1884. *Manual of the mosses of North America*. S. E. Cassino and Company, Boston. v + 447 pp. + VI pls.

Renauld, F. and J. Cardot. 1885. Notice sur les quelques mousses de l'Amérique du Nord. Rev. Bryol. 12: 44–47.

Wijk, R. van der, W. D. Margadant and P. A. Florschütz. 1967. Index muscorum. Volume IV (P–S). Regnum Veg. 48: 1–604.

Warnstorf, C. F. 1911. Sphagnales. Sphagnaceae. (Sphagnologia universalis). *In:* A. Engler, *Das Pflanzenreich, III* 51: i–iv, 1–546. Wilhelm Engelmann, Berlin.

Contr. Univ. Mich. Herb. 18:99–103. 1992.

WHAT IS LEJEUNEA TRIGONA?
(Studies on Lejeuneaceae subfam. Ptychanthoideae XXII)

S. Rob Gradstein
Institute of Systematic Botany
3584 CS Utrecht, The Netherlands

Lejeunea trigona was described by Montagne and Nees (1836) based on a liverwort specimen collected in Peru by the French traveller and palaeontologist Alcide d'Orbigny. The material consists of only a few stems, which according to the original description were taken from a lichen ("in *Parmelia speciosa* parasita"). Although the material is fertile and has both antheridia and perianths, there has been some confusion about the identity of *Lejeunea trigona,* presumably due to the poor condition of the type specimen. The authors of the *Synopsis Hepaticarum* (Gottsche, Lindenberg and Nees 1844–1847) considered the species to be most closely related to *Lejeunea chrysophylla* (Lehm.) Gott. *et al.*, an African taxon now placed in the genus *Acanthocoleus* (Kruijt 1988). Stephani (1911), however, treated *Lejeunea trigona* as a member of the genus *Archilejeunea.* More recently, *Lejeunea trigona* was studied by Kruijt (1985) who considered the species a synonym of *Lejeunea phyllorhiza* Nees 1833. The latter is a widespread neotropical species, which was usually placed in *Dicranolejeunea* but was transferred to *Brachiolejeunea* by Kruijt and Gradstein (1986).

In the course of my work on neotropical Lejeuneaceae for *Flora Neotropica,* I have recently had a chance to reexamine the material of *Lejeunea trigona.* It appears that the species has affinity neither to *Archilejeunea* nor to *Brachiolejeunea phyllorhiza.* The rather flat leaves with reduced leaf lobules and the smooth perianths without or with broadly rounded keels of *Lejeunea trigona* would rule out *B. phyllorhiza,* which has concave and more or less squarrose leaves with large, unreduced lobules, and sharply keeled, ciliate perianths surrounded by winged female bracts. Another important characteristic of *Lejeunea trigona* is its thin stem, which has a distinct hyaloderm and a ventral merophyte which is mostly only two cells across. Both *Brachiolejeunea* and *Archilejeunea* have broader ventral merophytes, being four or more cells wide. In *Archilejeunea,* moreover, a hyaloderm is lacking.

Because of its narrow ventral merophyte and other morphological features, *Lejeunea trigona* undoubtedly bears closest resemblance to members of the genus *Acanthocoleus* (subfam. Ptychanthoideae). This genus was recently segregated from *Dicranolejeunea* by Schuster (1970) and was subsequently monographed by Kruijt (1985, 1988) who recognized seven species, two of which occur in tropical America. Diagnostic characters of *Acanthocoleus* are its rather unspecialized stems, lacking a subepidermis and bulging epidermis characteristic of *Dicranolejeunea,* its untoothed female involucres, its creeping habit and its brownish color. A comparison of *Lejeunea trigona* with the species recognized in *Acanthocoleus* shows that it is different from all of them. Its most striking feature is the strongly inflated perianths which are barely keeled and completely smooth, lacking any trace of cilia. None of the species of *Acanthocoleus* has such perianths. Furthermore, the antheridia of *L. trigona* are borne singly in the axils of leaves just

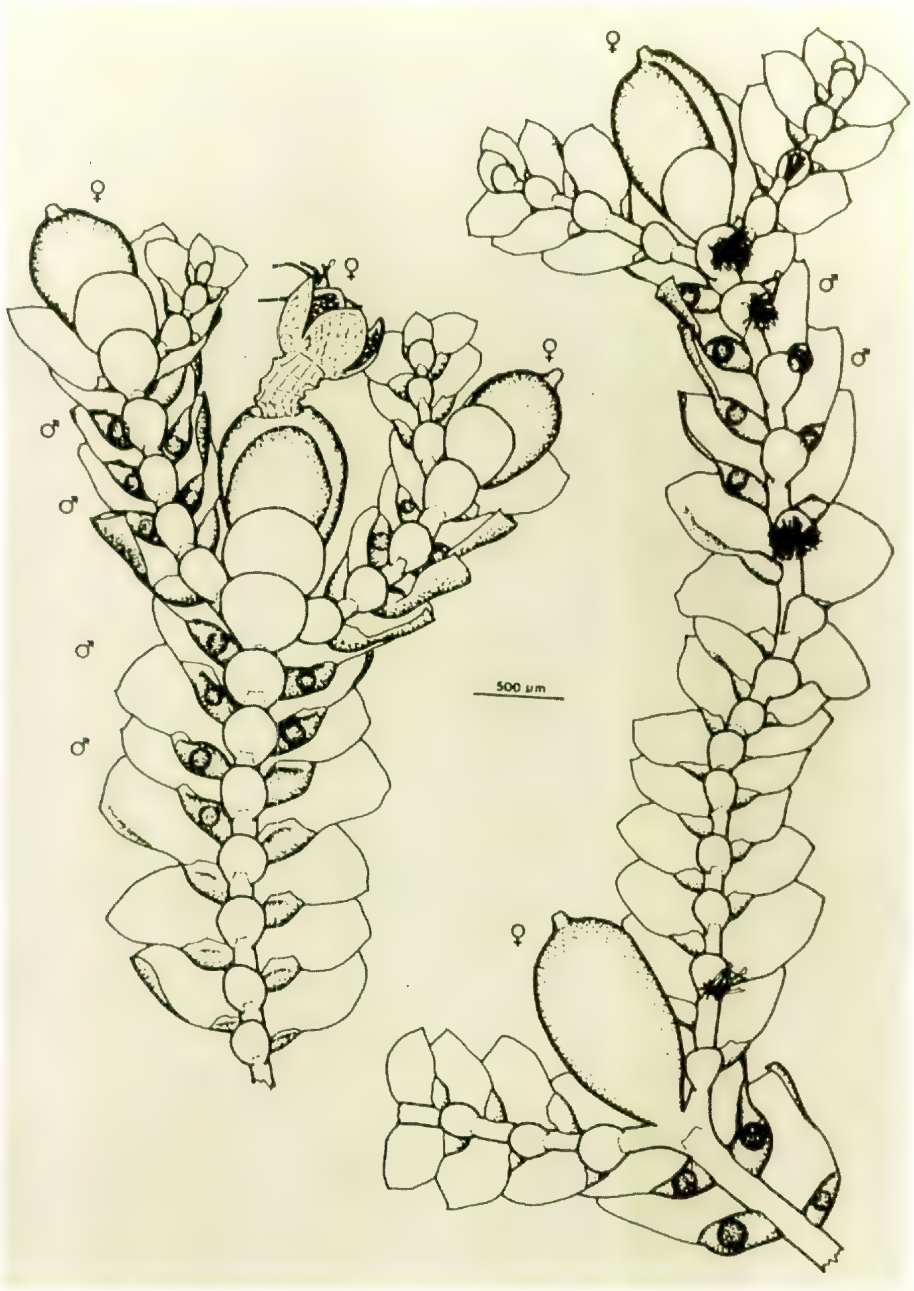


FIG. 1. *Acanthocoleus trigonus* (Nees & Mont.) Gradst.

below the perianth, and the species should thus be considered paroicous. Within *Acanthocoleus* a paroicous sex distribution is characteristic for *A. juddii* Kruijt from the Greater Antilles and Mexico, and *A. chrysophylla* (Lehm.) Kruijt from Africa. These two species are very different from *Lejeunea trigona*, however, by their keeled perianths with ciliate margins and their apiculate leaves. *Lejeunea trigona* thus appears to be a distinct species of *Acanthocoleus* and the following new combination may be proposed:

Acanthocoleus trigonus (Nees & Mont.) Gradst., comb. nov.

Lejeunea trigona Nees & Mont. *in* Montagne & Nees, Ann. Sci. Nat. Bot., Sér. 2, 5: 61. 1836; *Archilejeunea trigona* (Nees & Mont.) Steph., Spec. Hep. 4: 721. 1911. FIG. 1.

DISTRIBUTION

The distribution of *Acanthocoleus trigonus* has been remarkably poorly known and for more than a hundred years only the scanty type specimen from Peru has been available. As a happy coincidence, however, I have recently been able to rediscover the species in southern Bolivia (Dept. Tarija), during a collecting trip made in the company of my wife and the bryologist Marko Lewis, a curator at the National Herbarium of Bolivia in La Paz. *Acanthocoleus trigonus* proved to be quite common in humid *Podocarpus* forest remnants in mountain valleys, in areas with a prolonged dry season and at elevations between about 1600–2600 m. (FIG. 2). The species was always growing in thin mats on boulders along streams. In the field, the species could be easily recognized with a handlens by its peculiar perianths, which were often completely terete and devoid of keels. Searching through the unidentified liverwort materials of the herbarium in La Paz, I subsequently found further specimens of *A. trigonus* collected by Marko Lewis in the same general area. In addition, two further collections of *A. trigonus* have recently become available: one from southern Brazil, collected by Alfons Schäfer-Verwimp and his wife, and an older collection from northern Argentina (leg. Hosseus), described by Herzog as *Archilejeunea argentinica* Herz. (Feddes Repert. 55: 12. 1952). The latter should be considered a synonym of *Acanthocoleus trigonus*.

FIG. 2. Remnants of *Podocarpus* forest in mountain valleys at about 2000 m near Entre Rios, Dept. Tarija, southern Bolivia. *Acanthocoleus trigonus* occurs on rocks along streams in these forests.

It thus appears that *Acanthocoleus trigonus* occurs in relatively dry, subtropical mountain areas of South America (Peru, Bolivia, southern Brazil, northern Argentina), in regions with a seasonally dry climate. The Lejeuneaceae flora of this region is rather poor and most of the taxa reported are widespread, neotropical species. Among the Ptychanthoideae, *Acanthocoleus trigonus* is the only species endemic to this region. An explanation for the poor Lejeuneaceae flora of subtropical South America is probably the rarity in these areas of well-developed evergreen rain forests, which are the main habitat for the species of this family. Support for this assumption comes from a comparison between the Lejeuneaceae flora of South America and Australia (Thiers 1990, Gradstein 1991). As demonstrated by Thiers, the subtropical east coast of Queensland has a rich Lejeuneaceae flora with several endemic species. This high diversity is due to the occurrence in this region of rain forests, distributed in patches from north to south along the coasts of Queensland and New South Wales and ranging well into the temperate zone. These forests offer a great variety of habitats for inhabitation by Lejeuneaceae. A similar latitudinal gradient of rain forest is lacking in the New World, however, and this, then, may well account for the poverty of Lejeuneaceae in the subtropical regions of South America.

Key to the Neotropical Species of *Acanthocoleus*

1. Lobule large, ½–⅔× lobe length, rarely reduced, first tooth of the lobule 3–6 cells long; leaves orbicular; paroicous; Greater Antilles, Mexico, ca. 800–2500 m. ..... *A. juddii* Kruijt
1. Lobule smaller, ¼–⅖× lobe length, often reduced, first tooth 0–2 cells long; leaves ovate; autoicous or paroicous.
   2. Paroicous; perianth terete or very bluntly keeled, smooth; leaf apex rounded, entire; S Brazil, Peru, Bolivia, northern Argentina, ca. 1000–2600 m. ..... *A. trigonus* (Nees & Mont.) Gradst.
   2. Autoicous; perianth sharply keeled, ciliate; leaf apex pointed, rarely rounded, toothed or entire; throughout the neotropics, 150–2600 m. ..... *A. aberrans* (Lindenb. & Gott.) Kruijt

A full description of *Acanthocoleus trigonus* will appear in my forthcoming monograph of the neotropical Ptychanthoideae in *Flora Neotropica*.

Specimens examined. Peru. Laguna: Santa Cruz, "in *Parmelia speciosa*", *D'Orbigny s.n.*, type of *Lejeunea trigona* Nees & Mont. (STR, holotype; PC-Mont., isotype). Brazil. Santa Catarina: Serra do Corvo Branco, road Urubici-Crao Pará, just below the pass, Dec 1990, *Schäfer-Verwimp 13496* (hb. Schäfer-Verwimp, U). Bolivia. Chuquisaca: Río Jatum Mayu 14 km NW of Zudañez, *Lewis 84-0489* (LPB, U). Tarija: along road Tarija-Bermejo, ca. 10 km N of La Marmora, *Gradstein 7720, 7721* (LPB, U); headwaters of Río Los Pinos 20 km NW of Padcaya, *Lewis 84-2910* (LPB); headwaters Río Posta along road Tarija-Entre Rios 1950 m, *Gradstein 7648* (LPB, U); headwaters Río Huayco along road Narvaez-San Josecito, *Gradstein 7687* (LPB, U); along Río Tambo ca. 5 km S of Narvaez, *Lewis 84-2631, 84-2675* (LPB), *Gradstein 7651* (LPB, U); Cerro Sarzo, 4 km NW of Canaletas, *Lewis 84-2510* (LPB). Argentina. Córdoba: Ongamira, *Hosseus s.n.*, type of *Archilejeunea argentinica* Herz. (JE, holotype).

ACKNOWLEDGMENTS

I express my gratitude to Mariette Aptroot-Teeuwen for preparing the drawing of *Acanthocoleus trigonus* and to the curators of the herbaria cited for the loan of specimens.

LITERATURE CITED

Gottsche, C. M., J. B. Lindenberg and C. G. Nees von Esenbeck. 1844–1847. *Synopsis Hepaticarum.* Hamburg.

Gradstein, S. R. 1991. Diversity and distribution of Asian Lejeuneaceae subfamily Ptychanthoideae. Trop. Bryol. 4: 1–16.

Kruijt, R. 1985. A preliminary revision of the genus *Dicranolejeunea* (Spruce) Schiffn. Beih. Nova Hedwigia 80: 155–163.

———. 1988. A monograph of the genera *Dicranolejeunea* and *Acanthocoleus*. Bryophyt. Biblioth. 36: 1–135.

——— and S. R. Gradstein. 1986. On *Brachiolejeunea phyllorhiza* (Nees) Kruijt & Gradstein comb. nov. Nova Hedwigia 43: 299–309.

Montagne, J. P. F. C. and C. G. Nees von Esenbeck. 1836. Jungermanniearum herbarii Montagneani Species. Ann. Sci. Nat. Bot., Sér. 2, 5: 52–72.

Schuster, R. M. 1970. Studies on Hepaticae XLIX–LIII. New Lejeuneaceae from Dominica and Jamaica. Bull. Torrey Bot. Club 97: 336–352.

Stephani, F. 1911. *Archilejeunea. In: Species Hepaticarum* 4: 703–736. Geneva.

Thiers, B. 1990. An overview of the Lejeuneaceae in Australia. Trop. Bryol. 2: 273–283.

Contr. Univ. Mich. Herb. 18:105. 1992.

MOSSES AS USEFUL PLANTS

A. J. Sharp
Department of Botany
University of Tennessee
Knoxville, TN 37996–1100, U.S.A.

When the uses of mosses are mentioned, the ones usually thought of are the peat mosses (*Sphagnum* spp.). These have been used for centuries in the form of peat which when dried can be used as fuel furnishing heat in their habitations. It also was used as a dressing on open wounds in war, and also in forestry accidents. It contains sphagnol (an antiseptic phenolic compound), and when dried it is also very absorptive. This also led to its use as menstrual pads in the past.

Mosses are also collected for ornamental purposes in florist shops, and also are used in terraria which has led to the decimation of forest mosses in some places in the Southern Appalachians. In the streets and on store fronts of the villages in Mexico and Guatemala, pendant forms are frequently used for decorations during their festivities.

In nature, mosses growing on logs and decaying forest residue tend to hold moisture which facilitates the return of woody plants, and acts as fertilizer for the next plant crop.

Less well-known is the use of mosses by animals for food and other purposes. I call attention to the following in order that we may have a more thorough and scientific knowledge of another aspect of the significance of mosses in the natural environment.

Twice in the Southern Appalachians I have seen mice eating the sporangia of *Polytrichum* and *Pogonatum*. Unfortunately, I made no record of the exact locality and date. Several times in Alaska I have encountered lemming pathways which had been tunnels under the snow. Most of the mosses in these runways were devoid of capsules, and in some instances, the setae were missing. Again, I failed to record the name of the mosses, the locality, or the date. I am sure that one of the mosses was a *Ceratodon*.

This indicates that mosses can be of importance to some of our furbearers, foxes, wolves, and cats, that feed on rodents. Thus, a woman could be wearing a furpiece derived indirectly from mosses.

In another instance in Alaska I encountered a wasp nest in a relatively dry hummock of peat moss (*Sphagnum*). They pointedly let me know that it was their territory. Thus we have a moss home for wasps on which some predators feed. Again, I kept no locality or date.

I write this as a challenge for bryologists to record data that we need to understand the full importance of mosses in the environment.

I also write this as a salute to Dr. Howard Crum who was not afraid to tackle a big problem when he first worked on his Ph.D. dissertation concerning the mosses of Mexico.

Contr. Univ. Mich. Herb. 18:107–111. 1992.

STUDIES ON GEOCALYCACEAE VII. SUBSPECIFIC DIFFERENTIATION OF CHILOSCYPHUS SEMITERES TOGETHER WITH FURTHER REFINEMENTS IN CHILOSCYPHUS (S. LAT.)

John J. Engel
Department of Botany
Field Museum of Natural History
Chicago, IL 60605, U.S.A.

Chiloscyphus semiteres is a pan-south temperate species occurring in the Australasian, American and African sectors (Fig. 1). The species occurs in variable frequencies in different parts of its range. It is very rare in the Falkland Islands (Engel, 1990), probably lacking in the Magellanian zone of southern South America (I did not record it for the Brunswick Peninsula [Engel, 1978], and the few other Magellanian records are suspect), and somewhat common in the Valdivian zone and on Juan Fernández. In the African sector the species is restricted to Cape Province, South Africa, where apparently it is rather common judging from the number of specimen citations in Grolle (1959). The species is of variable frequency within Australasia: it is rather common in New Zealand, but in Tasmania and Australia *C. semiteres* is one of the most common or perhaps *the* most common hepatic. The species also occurs in the oceanic Isles of Scilly (Paton, 1965) and Scotland (Long, 1982).

Chiloscyphus semiteres is characterized by a) undivided, entire leaves that are broadly rounded to truncate at the apex; b) conspicuous, deeply divided underleaves that frequently are asymmetrically inserted and have the laminal margin on each side with a process grading from dentiform to lobuliform; and c) a variable gynoecial position: some to many on short lateral-intercalary branches lacking normal leaves, while others are on terminal branches and main shoots.

The species exhibits subspecific differentiation only in the Australasian sector, where it may be separated into two varieties as follows:

Key to Varieties of *Chiloscyphus semiteres*

1. Underleaf disc lateral armature well-developed: mostly laciniate to lobulate; trigones minute to small, only occasionally medium and straight-sided; underleaves often 1.5–3× stem width; plants translucent ..... *C. semiteres* var. *semiteres*
1. Underleaf disc lateral armature reduced: mostly dentiform to ciliiform or lacking, only sporadically small-laciniiform; trigones normally large and bulging to knotlike (in shade forms medium and straight-sided to weakly bulging); underleaves normally 1–1.5× stem width; plants dull-opaque ..... *C. semiteres* var. *canaliculatus*

Chiloscyphus semiteres (Lehm.) Lehm. & Lindenb. var. **semiteres**

Jungermannia semiteres Lehm., Linnaea 4: 363. 1829; *Chiloscyphus semiteres* (Lehm.) Lehm. & Lindenb. *in* G. L. & N., Syn. Hep. 190. 1845;

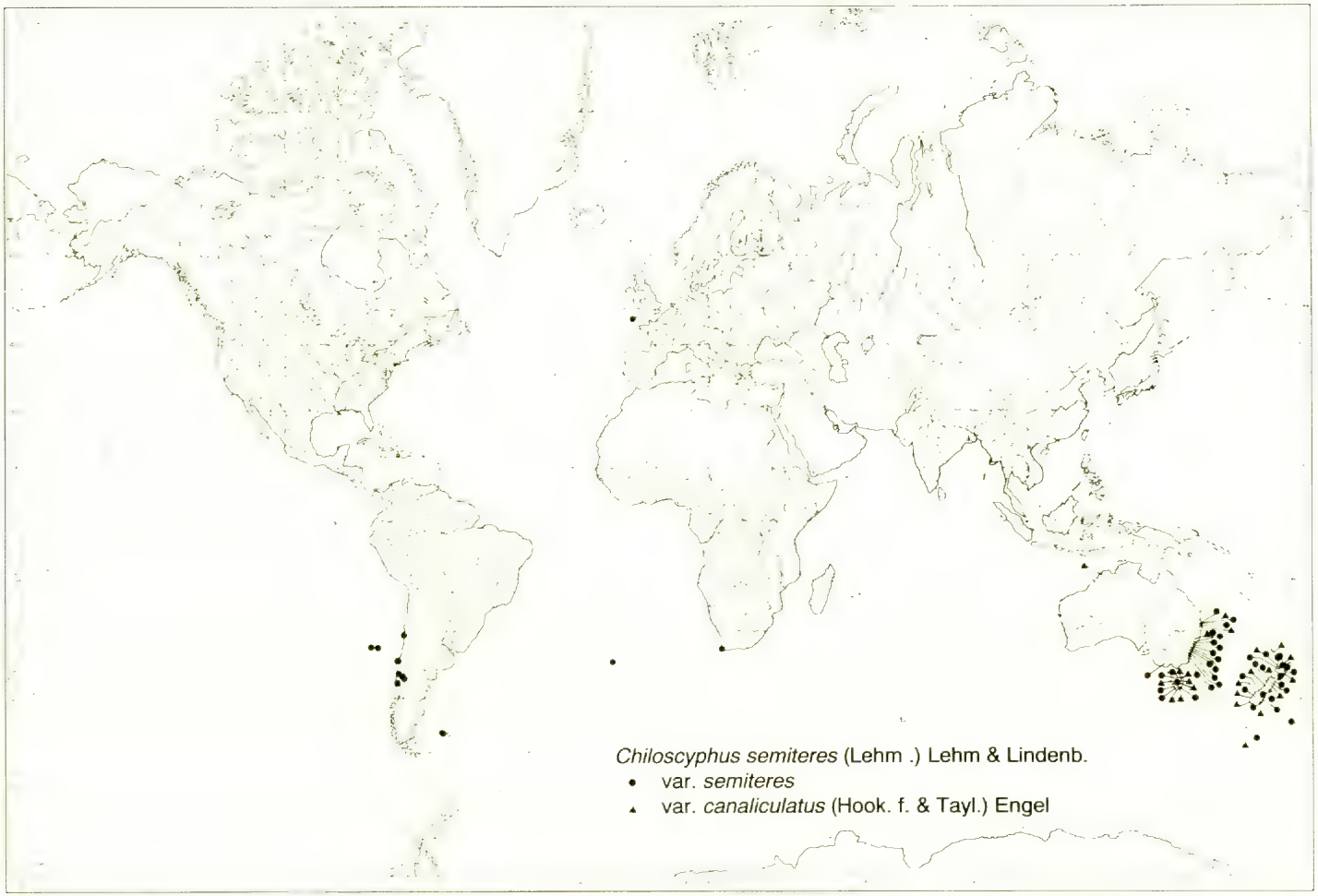


FIG. 1. Distribution of the two varieties of *Chiloscyphus semiteres*.

Lophocolea semiteres (Lehm.) Mitt., J. Linn. Soc., Bot. 16: 188. 1877. ORIGINAL MATERIAL. SOUTH AFRICA: Cape Prov., (Cap. Bonae Spei), "latere orientali montis Teufelsberg", *Ecklon* (G!).

Plants translucent. Trigones minute to small, occasionally medium and straight-sided, 2.4–4.8 μm, the ratio of trigone diameter to length of intervening thin wall between trigones 1:2–5.6. Underleaf disc often 1.5–2× stem width; the lateral armature well developed: mostly laciniiform, at times lobuliform.

Distribution: Pan-south temperate (FIG. 1).

Chiloscyphus semiteres var. **canaliculatus** (G. L. & N.) Engel, comb. & stat. nov.

Chiloscyphus canaliculatus G. L. & N., Syn. Hep. 710. 1847; *Jungermannia canaliculata* Hook. f. & Tayl., London J. Bot. 3: 563. 1844, *hom. illeg., non J. canaliculata* Nees, Hep. Javanicae 10. 1830; *Lophocolea heterophylloides* var. *canaliculata* (G. L. & N.) Carring. & Pears., Pap. & Proc. Roy. Soc. Tasmania 1887: 51. 1888; *Lophocolea canaliculata* (G. L. & N.) Steph., Bull. Herb. Boissier 6(9): 786. 1906 (= Spec. Hep. 3: 86). LECTOTYPE (*nov.*). NEW ZEALAND: "Falls of Waitangi", *Hooker s. n.* (FH!—c. per. + ♂).

Plants dull-opaque. Trigones normally large and bulging to knotlike, in shade forms medium and straight-sided to weakly bulging, (4.8–)6–7.2(–8.4) μm, the ratio of trigone diameter to length of intervening thin wall between trigones variable: 1:(0.9–)1.2–2.6(–3.2). Underleaf disc usually 1–1.5× stem width; the lateral armature reduced: mostly dentiform to ciliiform or lacking, only sporadically small-laciniiform.

DISTRIBUTION: New Zealand, Tasmania and southeast Australia (FIG. 1).

FURTHER REFINEMENTS IN CHILOSCYPHUS

1) SUBSPECIFIC DIFFERENTIATION OF *CHILOSCYPHUS NOVAE-ZEELANDIAE*

This polymorphic species occurs in New Zealand, Tasmania and southeast Australia. It may be subdivided into three units, as follows:

a) Chiloscyphus novae-zeelandiae var. **novae-zeelandiae**

Jungermannia novae-zeelandiae Lehm. & Lindenb. *in* Lehmann, Nov. Min. Cogn. Stirp. Pug. 6: 33. 1834; *Lophocolea novae-zeelandiae* (Lehm. & Lindenb.) Nees *in* G. L. & N., Syn. Hep. 168. 1845; *Chiloscyphus novae-zeelandiae* (Lehm. & Lindenb.) Engel & Schust., Nova Hedwigia 39: 420. 1984 [1985]. ORIGINAL MATERIAL. NEW ZEALAND: South Is., Dusky Bay, *s. coll.* [*Menzies*] (BM!, G!, S![2], ex hb. Hooker—c. per.).

b) Chiloscyphus novae-zeelandiae var. **meridionalis** (Steph.) Engel, comb. & stat. nov.

Lophocolea meridionalis Steph., Bull. Herb. Boissier 6(10): 888. 1906 (= Spec. Hep. 3: 113). ORIGINAL MATERIAL. NEW ZEALAND: "Insula meridionalis", Waimate (Canterbury), May 1901, *Beckett 2737* (G!–c. ♂).

c) **Chiloscyphus novae-zeelandiae** var. **grandistipulus** (Schiffn.) Engel, comb. & stat. nov.

Lophocolea grandistipula Schiffn. *in* Naumann, Forschungsr. Gazelle 4: 12, *pl. 3, f. 29–32*. 1890. ORIGINAL MATERIAL. NEW ZEALAND: Auckland, 8 Nov 1875, *Naumann* (FH!, sub *L. stipularis, nom. hb.)*.

2) *CHILOSCYPHUS PERPUSILLUS* COMB. NOV.

Chiloscyphus perpusillus (Hook. f. & Tayl.) Engel, comb. nov.

Jungermannia perpusilla Hook. f. & Tayl., London J. Bot. 3: 380. 1844; *Lophocolea perpusilla* (Hook. f. & Tayl.) G. L. & N., Syn. Hep. 163. 1845. ORIGINAL MATERIAL. NEW ZEALAND: Campbell Is., *Hooker* (BM![4], FH!).

3) THE TAXONOMIC POSITION OF *CHILOSCYPHUS STRIATELLUS* MASS.

This species occurs in both the Valdivian and Magellanian zones of southern South America. It has elongate, longitudinally oriented lamellae on the stem, and I am unaware of any other member of Jungermanniales with such processes. It belongs in a section of its own, as follows:

Chiloscyphus sect. **Striatelli** Engel, sect. nov.

Folia caulina et amphigastria caulina profunde bilobata, superficiebus levibis. Caulis lamellis parallelis, longitudinalibus, latitudine 2–5 cellularibus ornata.

Type: *Chiloscyphus striatellus* Mass.

Leaves and underleaves deeply bifid, smooth. Stems on all sides with parallel, longitudinal lamellae 2–5 cells high.

4) THE TAXONOMIC POSITION OF *CHILOSCYPHUS APOSINENSIS* PIIPPO

Chiloscyphus aposinensis of China is similar to the pan-tropical *C. muricatus* (Lehm.) Engel & Schust. of sect. *Microlophocolea* Spruce in having spinose leaf surfaces and deeply divided leaves and underleaves, but differs from that species in 1) the form of the leaf spines (the lumen of each protuberance is confluent with that of the subtending laminal cell and not separated from it by a cross wall [fig. 4 in Chang & Gao, 1984]); 2) the placement of leaf spines only on the dorsal surface of the leaf; and 3) the dense clusters of spines at the dorsal base of each leaf (fig. 4 in Chang & Gao, 1984). *Chiloscyphus aposinensis* belongs in an independent section, as follows:

Chiloscyphus sect. **Aposinenses** Engel, sect. nov.

Folia caulina pagina dorsali spinosa; spinae dispersae (cellula quaque spina unica ornata), sparsae ad basin ventralem, dense fasciculatae ad basin dorsalem, digitiformes, luminibus confluentibus cum luminibus laminae; folia caulina pagina levi instructa.

TYPE. *Lophocolea chinensis* Gao & Chang, Bull. Bot. Res. 4: 87. 1984 ≡ *Chiloscyphus aposinensis* Piippo (cf. Piippo, 1990).

Dorsal leaf surface spines scattered, 1 each per cell, sparse at ventral base, in dense clusters at postical base, fingerlike, the lumina confluent with that of lamina; ventral leaf surface smooth.

ACKNOWLEDGMENTS

I am grateful to Dr. Rolf Singer for assistance with the Latin diagnoses.

LITERATURE CITED

Engel, J. J. 1978. A taxonomic and phytogeographic study of Brunswick Peninsula (Strait of Magellan) Hepaticae and Anthocerotae. Fieldiana, Bot. 41: i–viii, 1–319.

———. 1990. Falkland Islands (Islas Malvinas) Hepaticae and Anthocerotophyta: A taxonomic and phytogeographic study. Fieldiana, Bot. N. S. 25: i–viii, 1–209.

Chang, Kuang-chu and Chien Gao. 1984. Plantae novae hepaticarum sinarum. Bull. Bot. Res. 4: 83–99.

Grolle, R. 1959. Beitrag zur Kenntnis der afrikanischen Lophocoleen. Trans. Brit. Bryol. Soc. 3: 582–598, pl. 1–3.

Long, D. G. 1982. *Lophocolea semiteres* (Lehm.) Mitt. established in Argyll, Scotland. J. Bryol. 12: 113–115.

Paton, J. A. 1965. *Lophocolea semiteres* (Lehm.) Mitt. and *Telaranea murphyae* sp. nov. established on Tresco. Trans. Brit. Bryol. Soc. 4: 775–779, f. 1.

Piippo, S., 1990. Annotated catalogue of Chinese Hepaticae and Anthocerotae. J. Hattori Bot. Lab. 68: 1–192.

Contr. Univ. Mich. Herb. 18:113–130. 1992.

A REVISION OF OCHROBRYUM (LEUCOBRYACEAE)

Bruce Allen
Missouri Botanical Garden
P.O. Box 299
St. Louis, MO 63166–0299, U.S.A.

DEDICATION

Not so long ago I began to learn moss taxonomy with a copy of Howard Crum's *Mosses of the Great Lakes Forest,* a gift from Ronald Pursell. My continued interest in mosses, to a great extent, is due to my beginning with that special book. I am, therefore, especially grateful to be able to contribute the following paper to this Festschrift honoring Howard Crum.

INTRODUCTION

Ochrobryum was established by Mitten (1869) for two leucobryaceous mosses with short, immersed capsules. The genus has a bizarre sporophytic complex that is unique in the Leucobryaceae: a short seta, a hemispherical, eperistomate capsule, and a short, symmetrical, rostrate operculum tightly enclosed by an exceedingly long (to three times the length of the operculum), narrowly subulate, mitrate calyptra. In form the capsule and the operculum are so similar that the former has been described as "an inverted operculum . . ." (Robinson 1990). The calyptra, which may or may not be fringed at base by long unicellular hairs, is generally longer than the combined operculum, capsule and seta. At capsule dehiscence the operculum commonly remains inside the calyptra. The resulting operculum/calyptra complex, although longer, has the same form as the deoperculate sporophyte.

The leaves of *Ochrobryum* have the alternating leucocyst/chlorocyst arrangement typical for the Leucobryaceae. Unlike many members of the family the leaves at base are nearly always three layered: one dorsal leucocyst layer, a central chlorocyst layer and one ventral leucocyst layer. Occasionally, the unistratose pattern in the dorsal layer is disrupted by the subdivision of one or two dorsal leucocysts. But, this is a non-typical event and leaves that are three-layered at base represent an essential feature of *Ochrobryum.* Three-layered leaves are also found in a few *Leucobryum* species, and in the neotropics *Ochrobryum* is frequently misidentified as *L. martianum* (Hornsch.) Hampe, a three-layered leaf species that otherwise has little resemblance to *Ochrobryum.*

In general, *Ochrobryum* leaves have ventral leucocysts positioned opposite the dorsal leucocysts. As a result the chlorocysts are four-sided. The chlorocysts proximally are isocentric, i.e., as close to the dorsal surface as to the ventral surface. However, as noted by Cardot (1900), the chlorocysts distally are hypocentric, i.e., closer to the dorsal surface than to the ventral surface. This hypocentric chlorocyst pattern is caused in two ways: all *Ochrobryum* species have enlarged upper ventral leucocysts, and in some species the upper ventral leucocysts are multilayered. The degree of chlorocyst hypocentricity is greater in these latter species than in the species with only enlarged leucocysts. Commonly, the species with multilayered

upper ventral leucocysts have fleshy or swollen leaf apices that are obtusely triangular in cross-section.

In past treatments of *Ochrobryum* leaf apex form has been used as a primary taxonomic character at the species level. This character, though useful, is astoundingly variable within single collections of some species. Consequently, it is best regarded as a secondary taxonomic character. The greatest variability in apical leaf form is found in those species that have multilayered upper ventral leucocysts (*O. gardneri* (C. Müll.) Mitt. and *O. kurzianum* Hampe *in* Besch.). In these species most leaves have fleshy, broadly acute to obtuse leaf apices. However, nearly all collections have some sharply acute leaves. Commonly, in these species the lower leaves are sharply to broadly acute while the upper leaves are fleshy and obtuse. For the species having only enlarged upper ventral leucocysts or a multi-layered pattern for only a single cell width (*O. subulatum* Hampe *in* Besch., *O. sakalavum* Card. & Par., and *O. sessile* Allen) the leaf apices are generally more sharply acute (obtuse in *O. sakalavum*) and not fleshy or swollen. Since all species of *Ochrobryum* have at least a few leaves with some type of acute apex, the use of leaf apical form as a distinguishing feature must always be accompanied by subjective qualifiers such as "most" or "some".

An interesting and characteristic feature of the leaves in *Ochrobryum* is the appearance of the upper chlorocysts. Distally the chlorocysts are short, and form chains of rounded to quadrate cells. This feature is well-developed in all *Ochrobryum* species and its presence is of critical importance in recognizing the genus when sporophytes are absent. Unfortunately, the feature is not unique to *Ochrobryum;* Cardot (1900) noted it in a number of *Leucobryum* species and considered the Leucobryaceae to commonly have chlorocysts that are wider toward the apex than toward the base. In this regard it should be noted that *Leucobryum incurvifolium* C. Müll. (one of the few *Leucobryum* species with erect capsules) has this chlorocyst feature as equally well-developed as any species of *Ochrobryum.*

Globose, budlike propagula were not attributed to *Ochrobryum* until 1901 (Geheeb 1901). Robinson (1990) considered these propagula to be a feature that uniquely defined the genus within the Leucobryaceae. All species in the genus, except *O. sakalavum* which is known only from a scanty type collection, possess propagula of this type. Generally the propagula end in a single blunt cell, however some species have propagula that end in a sharp cell. But, even in these latter species a few propagula with blunt terminal cells can also be found. The globose propagula are attached at their proximal ends to a central, reddish-brown stalk of variable length by an elongated cell. The position at which the propagula occur on the plant is a character of primary taxonomic significance at the species level. The propagula may be borne on the upper dorsal surface of the leaves, in globose masses at the end of a specialized, apical stalk, or clustered in the leaf axils.

Although *Ochrobryum* is largely defined by its sporophytic complex, the complex within the genus is nearly uniform. The only character in the complex that varies greatly is the degree and type of fringing of the calyptral base. In three species, *O. subulatum* (Asia, South America, Africa), *O. kurzianum* (Asia), and *O. sakalavum* (Madagascar) the base of the calyptra is densely beset with long, single-celled fringe cells. In the other species, *O. gardneri* (Central and South America, Africa) and *O. sessile* (Central and South America), the calyptra base may be weakly fringed or simply laciniate. In *O. gardneri* both fringed and laciniate calyptrae can be observed in the same collection.

Long, single-celled, fringed calyptrae are widely and sporadically found within

the Dicranaceae, Leucobryaceae, Hookeriaceae and Daltoniaceae. The unsuitability of this character as an indicator of natural relationships outside of a generic context is obvious from the fact that the calyptral fringe cells of *Ochrobryum* are identical in morphology and position to those found scattered in many genera in these families. Even the variable nature of the calyptral fringing in *Ochrobryum* has a counterpart in some species of *Campylopus* where fringed and un-fringed calyptrae can be found within single collections. Robinson (1990) considered fringed calyptrae in the Leucobryaceae (*Schistomitrium* and *Ochrobryum*) to be a localized apomorphy because of its sporadic occurrence within the family.

The erect capsules and mitrate calyptrae of *Ochrobryum* have led to the view that the genus is closely related to *Schistomitrium* (Mitten 1859, Andrews 1947). Further gametophytic support for this view is found in the hypocentric upper chlorocysts of *Ochrobryum*. As noted above, some species of *Ochrobryum* have leaf apices with enlarged, multilayered leucocysts. These leaf apices are essentially identical to the leaf apices found in species of *Schistomitrium* where this type of leaf apex represents a generic feature.

Robinson (1990) considered the generic subgroup of *Schistomitrium*, *Cladopodanthus* and *Holomitriopsis* to be the only Leucobryaceae-subgroup marked by more than one synapomorphy—mitrate calyptrae, hypocentric chlorocysts, and erect capsules. *Ochrobryum* has all three of these character states and clearly belongs within the complex. Indeed it appears better placed there than *Holomitriopsis* which has a cucullate calyptra. Robinson (1990) did not include *Ochrobryum* in the complex because of its unusual sporophyte and its globose vegetative propagula. As treated here these features are considered indicators of generic rather than subfamilial rank.

Ochrobryum was revised by Bescherelle (1897). This revision added fourteen species and one variety to the genus, many of which were sporophytically unknown. Cardot (1900) considered *Ochrobryum* and *Leucobryum* gametophytically inseparable and so transferred or excluded Bescherelle's species known only from gametophytic material. Cardot recognized nine species of *Ochrobryum* distributed in southern Asia and South America. Subsequently, the genus has been discovered in Central America and Africa. Wijk *et al.* (1964) attributed 20 taxa to the genus. Robinson (1965) added another species, but since he also transferred a Sri Lankan species of *Ochrobryum* to *Leucobryum*, 20 species are currently recognized in the genus.

TAXONOMIC TREATMENT

Ochrobryum Mitt., J. Linn. Soc., Bot 12: 107. 1869.—Type: *Leucophanes gardneri* C. Müll., Bot. Zeit. 2: 741. 1844.

Plants small, 3–20 mm high, pale-green to whitish. Stems red to reddish-brown, erect, simple or sparingly branched, commonly with numerous arrested branch primordia along all sides; in cross-section cells thin- to firm-walled, epidermis undifferentiated, central strand absent. Rhizoids of two types: stout, smooth, sparsely and irregularly branched, dark red to red-brown ones distributed on all sides of the stems at base; and slender, smooth to lightly roughened, at times pinnately branched, pale reddish-brown ones on stems above and below leaf insertions and at times from the dorsal sides of the leaf apices. Pseudoparaphyllia absent. Paraphyllia

absent. Leaves erect-incurved, erect-spreading to flexuose, channeled; margins entire; lamina narrow, restricted to the lower half of the leaf; in cross-section at base with a median row of quadrate chlorocysts and single layers of dorsal and ventral leucocysts, at leaf apex chlorocysts hypocentric, and having one or several layers of enlarged ventral leucocysts; chlorocysts short in the upper region of the leaf, forming chains of rounded or quadrate cells; alar cells not differentiated. Axillary hairs delicate, 4–6 cells: basal cell short rectangular, hyaline to gray, upper cells long rectangular, hyaline, terminal cells rounded at the apex. Asexual reproduction by means of globose propagula clustered on short stalks: 1) on dorsal surface of leaf towards the apex, 2) on apex of specialized terminal branch or stem extension, 3) in leaf axils, and 4) on slender rhizoids at base of stems. Dioicous. Perigonia terminal on short branches at apex of stem. Perichaetia terminal on stem, archegonia 800 μm long, with slender, elongate neck 550 μm long. Setae short, smooth, vaginula well developed; capsules immersed to shortly exserted, hemispheric to obconic, wide-mouthed when dry; annulus non-revoluble, consisting of several rows of thick-walled irregularly shaped cells at operculum and capsule mouth and two rows of long rectangular, yellowish, thin-walled cells at site of separation; stomata absent; opercula long-rostrate; peristome absent. Calyptra long-rostrate, the rostrum more than twice the operculum length, mitrate (occasionally splitting irregularly and appearing cucullate), laciniate or ciliate-fringed at base.

Etymology. A combination of the Greek *ochros* (pale, sallow, pale-yellow) and *bryon* (moss).

Distribution. Central America: Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, and Panama. South America: Colombia, Venezuela, Brazil, and Bolivia. Africa: Guinea, Zaire, and Madagascar. Asia: India, Nepal, Burma, Thailand, Cambodia, and Malaysia.

KEY TO THE SPECIES OF *OCHROBRYUM*

1. Leaves linear to setaceous, gradually narrowed from base to apex; apices mostly sharply acute, usually a few apices broadly acute ..... 2.
1. Leaves lanceolate, narrowly ovate at base; apices broadly acute or obtuse, both types in same collection ..... 3.
   2. Propagula clustered in leaf axils; apical ventral leucocysts frequently two-layered in the middle for a single cell width ..... *4. O. sessile.*
   2. Propagula clustered at tip of propaguliferous branch or stem extension which has reduced leaves; apical ventral leucocysts in a single layer ..... *5. O. subulatum.*
3. Leaves with apical ventral leucocysts two-layered in the middle for a single cell width; leaf lamina narrow at base, 2–4 cells wide ..... *3. O. sakalavum.*
3. Leaves with apical ventral leucocysts bi- to multi-layered in a broad band; leaf lamina broad at base, 4–10 cells wide ..... 4.
   4. Propagula on upper, dorsal leaf surface; basal leaf laminae with 4–6 layers of long-rectangular cells; plants of the neotropics and Africa ..... *1. O. gardneri.*
   4. Propagula clustered in leaf axils; basal leaf laminae with 6–10 layers of long-rectangular cells; plants of Asia ..... *2. O. kurzianum.*

1. Ochrobryum gardneri (C. Müll.) Mitt., J. Linn. Soc., Bot. 12: 108. 1869, "gardnerianum" see nomenclatural note 1. *Leucophanes gardneri* C. Müll., Bot.

Zeit. 2: 741. 1844. *Schistomitrium gardnerianum* (C. Müll.) Mitt., J. Proc. Linn. Soc., Bot. Suppl. 1: 26. 1859. TYPE. BRAZIL. *Gardner 94* (BM, H, NY isotypes).

Leucophanes gardnerianum C. Müll., Syn. Musc. Frond. 1: 85. 1849, *ortho. var.*

Leucobryum obtusifolium C. Müll., Bot. Zeit. 15: 577. 1857. *Schistomitrium obtusifolium* (C. Müll.) C. Müll., Ann. Sci. Nat. Bot., Sér. 5, 3: 339. 1865. *Ochrobryum obtusifolium* (C. Müll.) Mitt., J. Linn. Soc., Bot. 12: 108. 1869. TYPE. COLOMBIA. Santa Martha, Minca, *Funck & Schlim in coll. Linden 913* (BM, BR, H, NY isotypes), *syn. nov.*

Ochrobryum phyllanthum Lindb. *in* Besch., J. Bot. (Morot) 11: 141. 1897, *nom. nud. in synon.* Based on BRAZIL, environs de Caldas, juillet 1854, *Lindberg* (BM).

Ochrobryum paulense Broth. & Geh. *in* Geh., Rev. Bryol. 28: 11. 1901. TYPE. BRAZIL. São Paulo: near Apiahy, *Puiggari 561* (H isotype), *syn. nov.*

Ochrobryum normandii Card. & Par. *in* Par., Rev. Bryol. 29: 65. 1902. TYPES. GUINEA. Fouta Djallon: près Donhol Neera, 29 mars; entre Dango & Bouna, 30 mars; Bourrougal Tope, 2 avril; près riv. Kaligourou, 29 avril; all collected in 1901 by *Normand* (types not seen, see nomenclatural note 2), *syn. nov.*

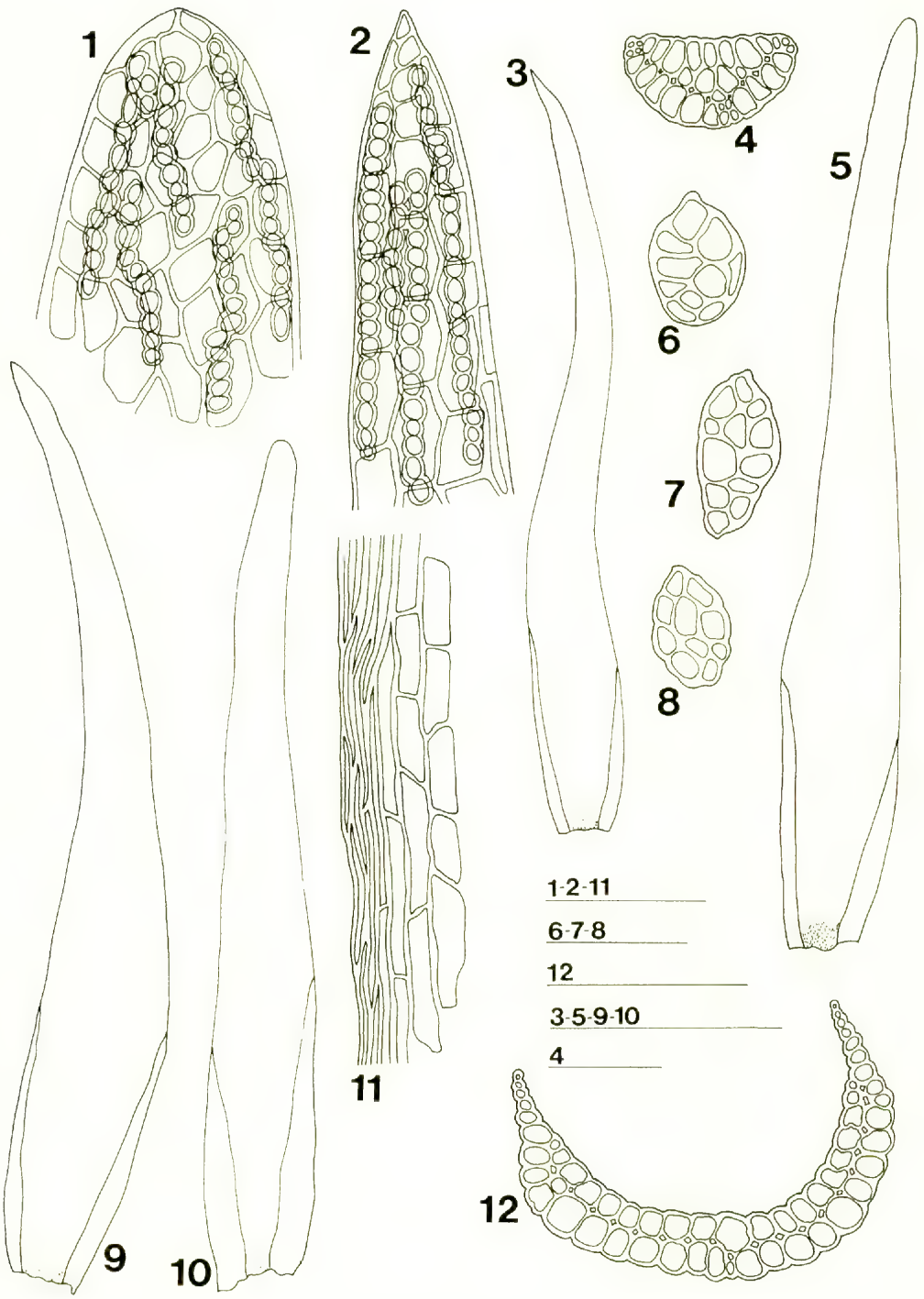
Ochrobryum dendeliae Broth. & Par. *in* Par., Rev. Bryol. 31: 117. 1904. TYPE. GUINEA. Ad arbores secus amnem Dendeli, 4 mart 1904, *Pobeguin* (BM, H, NY isotypes), *syn. nov.*

Ochrobryum crumii Robins., Bryologist 68: 92. 1965. TYPES. MEXICO. Jalisco: La Cumbre, 10 mi SW of Autlán, *Crum 1247* (US holotype; F, NY isotypes). PARATYPES. MEXICO. Jalisco, *Crum 438a* (MICH, not seen), *1334* (US), *syn. nov.*

Nomenclatural notes.

1. Wijk *et al.* (1964) incorrectly attributed the combination *O. gardneri* to Lindberg (1872) rather than Mitten (1869). This error can be attributed to Müller's (1849) use of an orthographic variant (*gardnerianum*) for a listing of his previously described *Leucophanes gardneri.* Müller never intended *L. gardnerianum* to be a new species as is evidenced by his direct reference in the species citation to his earlier paper. Mitten (1869) unfortunately used Müller's orthographic variant when transferring the species to *Ochrobryum.* In accordance with Article 75.3 (Greuter 1988) the epithet should be automatically corrected. In fact, it would seem that Lindberg (1872) was not effecting a transfer of the species but simply rectifying an orthographic error as can be seen from his citation of the species: *O. gardneri* (C. Müll.) Mitt.
2. The types of *O. normandii* were not available for study. Nevertheless, it is synonymized with *O. gardneri* on the basis of Cardot's statement (*in* Paris 1904) that the type of *O. maclaudii* is a mixture of that species (the fertile plants) and *O. normandii* (the sterile plants). My examination of this type material reveals a mixture of *O. subulatum* (fertile plants) and *O. gardneri* (sterile plants).

Plants in compact tufts or cushions, greenish-white, becoming whitish-brown with age. Stems 3–13(–20) mm high. Leaves 2–5 mm long, 0.3–0.8 mm broad, closely and densely erect-patent or stiffly patent-spreading, narrowly ovate-lanceolate to lanceolate, shortly acuminate, bluntly acute or rounded obtuse, at times cucullate, frequently apiculate; margins erect; leaf lamina narrow, consisting of 2–4 rows of long-rectangular, variously porose cells at midleaf and 4–6 rows of rectangular, firm-walled cells at base; costa with a single dorsal leucocyst-layer and a single ventral leucocyst-layer throughout most of the leaf; apical ventral leucocysts multi-layered. Asexual reproduction by brown, multicellular, globose propagula



FIGS. 1–12. *Ochrobryum gardneri*. 1 & 2. Leaf apices. 3, 5, 9, 10. Leaves. 4. Leaf cross-section at apex. 6–8. Globose propagula. 11. Basal leaf lamina. 12. Leaf cross-section at base. Scales in mm: 1, 2 & 5 = 0.1; 3 = 0.2; 4 = 1.0. Figs. 1, 2, 4, 8, 11, 12 from *Gardner 94;* figs. 3, 5, 6, from *Crum 1247;* figs. 7, 9, 10 from *Linden 913*.

clustered on short stalks on the upper dorsal leaf surface. Setae smooth, 1.0–1.5 mm long; capsules immersed to emergent, 0.5–1.0 mm long; opercula 1.5 mm long. Calyptrae 4–5 mm long, ciliate or laciniate at base. Spores spherical, smooth or lightly roughened, 12–18 μm.

Distribution. Central America (Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, and Panama); South America (Colombia, Brazil, and Bolivia); Africa (Guinea).

Illustrations. Bescherelle (1897, figs. 1, 5); Cardot (1900, plate 8, fig. 37); Bartram (1949, fig. 31, A–D); Robinson (1965, figs. 15–21); Yano (1975, fig. 28, a–g); Figs. 1–12.

Habitat. On rotting logs or tree trunks, and on bark at base of trees; 105–2200 m.

Specimens examined. CENTRAL AMERICA. Mexico. Chiapas: above Mapastepec, *Sharp 4409* (US); Colima: Alzada, *Orcutt 5359* (FH); Jalisco: La Cumbre, *Crum 1247* (F, NY, US). Guatemala. Alta Verapaz: Cobán, *Türckheim* (NY); Baja Verapaz: near Jicaro, *Sharp 2660a* (FH). Honduras. Olancho: 14°54′N; 85°56′W, *Olson 83-7b* (MO). Nicaragua. Jinotega: near Jinotega, *Standley 9566* (F). Costa Rica. San José: Santa María de Dota, *Standley & Valerio 43142* (FH, NY, US), *Standley 41628* (FH, H, US), *Standley 41651* (FH, US). Panama. Chiriquí: 8°35′N, 81°45′W, *Allen 5218* (MO), Santa Clara, *Mori & Bolten 7169* (MO), 2 mi S of Boquete, *Crosby 3961* (MO, PMA), Cerro Pando, 8°52′N, 82°45′W, *Hamilton et al. 811* (MO), 2 mi E of Boquete, *Nee 10804* (MO, NY, PMA, US).

SOUTH AMERICA. Colombia. Magdalena: Santa Marta, *Linden 913* (BM). Brazil. Bahia: 11°39′S, 41°07′W, *Vital 8038* (MO); Goiás: Serra Geral do Paraná, *Irwin et al. 31982 p.p.* (FH, H, NY), *Irwin et al. 33185* (FH, H, NY), *Irwin 33208a* (NY); Minas Gerais: Caldas, *Mosén* (H), Lagoa Santa, *Warming* (BM); São Paulo: Faxima, *Puiggari 561* (H). Bolivia. La Paz: Santa Anna, Apolo region, *Williams 1861* (BM, FH, H, NY); Santa Cruz: Velasco Province, Río Blanco, *Herzog* (H), Prov. Velasco, 15°58′S, 61°05′W, *Lewis 85-1036* (MO).

AFRICA. Guinea. Féfiné River, *Maclaud p.p.* (BM); Lambeira, *Pobequin* (BM, NY); Dombiagni, *Pobeguin* (H, NY); Dendeli, *Pobeguin* (H); Diendieu, *Pobeguin* (NY).

This species and *O. kurzianum* form a close pair marked by the presence of bluntly acute to obtuse leaves that are distinctly swollen or thickened at the extreme apex due to their enlarged and multi-layered upper ventral leucocysts. *Ochrobryum kurzianum* differs in having propagula clustered in the leaf axils and by its better developed leaf laminae (6–10 layers of long rectangular cells). The two species are geographically distinct: *O. gardneri* Central America, South America and Africa; *O. kurzianum* Asia.

The leaf apices in *O. gardneri* are remarkably variable, even within single collections. At times nearly all leaves are obtuse and apiculate, conversely some collections have mostly broadly acute leaves. All collections have leaves with thickened apices and at least some obtuse leaves. Globose propagula borne on the upper dorsal leaf surface are a constant, diagnostic feature of *O. gardneri.*

This species is similar to *O. sessile* which is sympatric with it in Central America and northern South America. *Ochrobryum sessile* has moderately stout leaves with leaf apices that approach those of some plants of *O. gardneri.* In addition, the leaf apices frequently have ventral leucocysts in a two-layered pattern for a single cell width in the middle of the leaf. *Ochrobryum sessile* differs not only by its lack of an extensive apical region of multilayered ventral leucocysts, but also by having propagula clustered in the leaf axils and smoothly tapered, narrower, more sharply acute leaves.

Ochrobryum subulatum frequently occurs mixed with *O. gardneri.* It is a more slender plant with narrowly acute leaves, a constant uni-layered ventral leucocyst

pattern, and has globose leaf propagula on specialized, terminal branches or stem extensions.

Vegetatively this species resembles *Leucobryum polakowskyi* (C. Müll.) Card. or *L. incurvifolium*. But, these two species proximally have multi-layered dorsal and ventral leucocysts, quadrate basal laminal cells, and they reproduce asexually by means of terminal clusters of reduced leaves.

Holomitriopsis laevifolia (Broth.) H. Robins., a Venezuelan species with obtuse, apiculate leaves and a single dorsal and ventral leucocyst-pattern, may also approximate this species. *Holomitriopsis laevifolia* is a more robust plant, lacks rounded to quadrate apical chlorocysts and leaf propagula, has a cucullate calyptra, and a peristomate capsule.

2. Ochrobryum kurzianum Hampe *in* Besch., J. Bot. (Morot) 11: 145. 1897. TYPES. BURMA. Moulmein, *Stoliczka* [*Kurz*] *4434* (BM lectotype; BM, BR, H isolectotypes), *Stoliczka* [*Kurz*] *4438* (BM, H syntypes); Pegu-Yomah, *Kurz 2890* (BM, H, NY syntypes); Martaban, *Kurz 2842* (BM, H, NY syntypes).

Ochrobryum kurzianum Hampe *in* F. Mason, Burma 2: 49. 1883, *nom. nud.*

Ochrobryum nepalense Besch., J. Bot. (Morot) 11: 145. 1897. TYPE. NEPAL. *Wallich 30* (BM holotype; BM isotypes), *syn. nov.*

Ochrobryum parishii Besch., J. Bot. (Morot) 11: 142. 1897. TYPE. BURMA. Moulmein, *Parish 2* (BM holotype; NY isotype), *syn. nov.*

Nomenclatural notes.

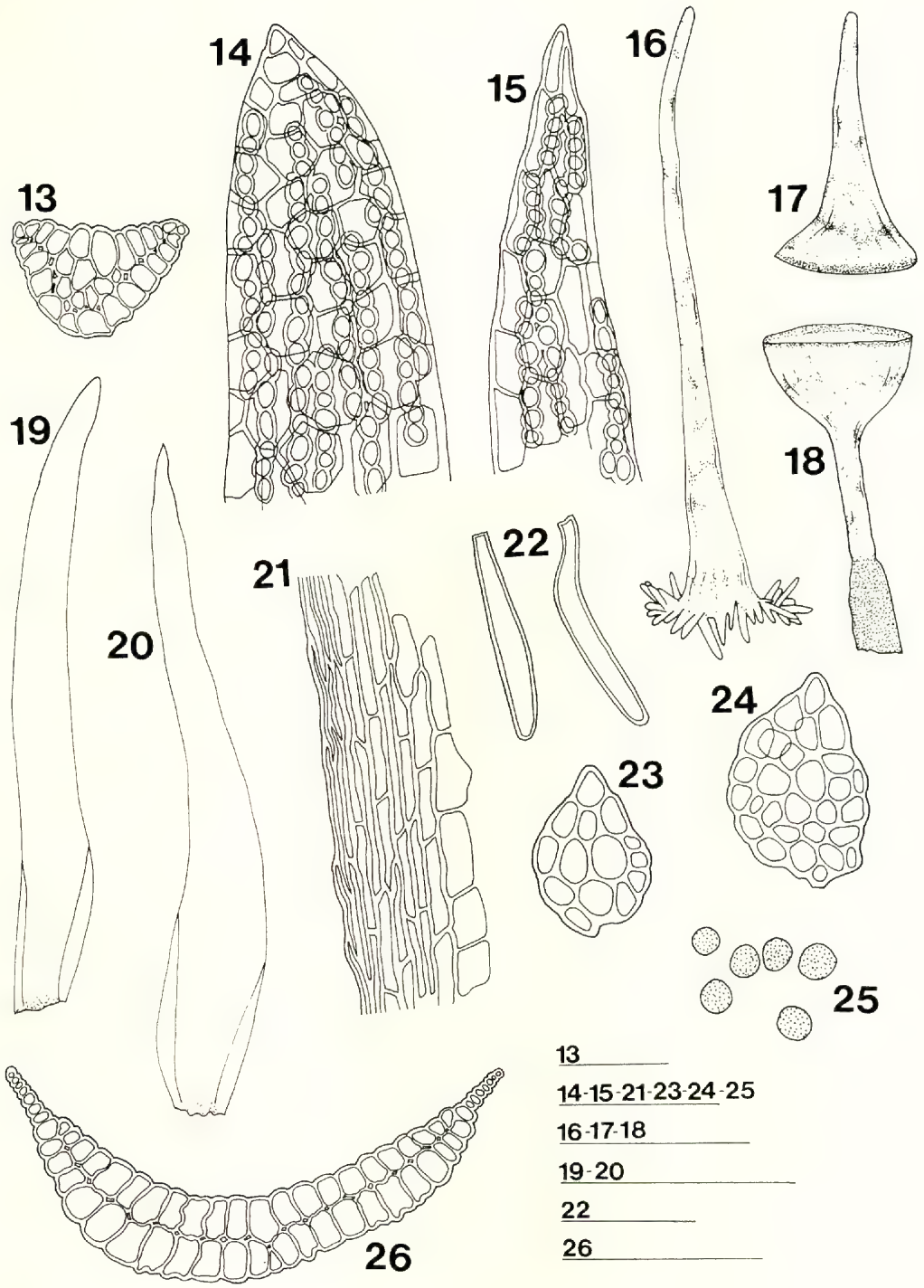
1. The above three species have equal priority. The epithet *kurzianum* is used for the combined taxon since it is the name in common use in Asia.
2. The lectotype of *O. kurzianum* (the only type material in the Bescherelle herbarium) was cited as "*Stoliczka, S. Kurz 4434*" (Bescherelle 1897), but the specimen in Hampe's herbarium was evidently collected solely by Stoliczka. Hampe's specimen has one of Kurz's printed labels on which Stoliczka's name has been hand-written and Kurz's name crossed out.
3. The type of *O. parishii* is *Parish 2*, but specimens at BM and NY with the number 22 may also be type material. The error may have occurred when Mitten (1856) listed *Parish 2* as "22. *Schistomitrium garderianum*"; in the same paper *Parish 22* is a hepatic. The holotype has no collection number. In the Mitten herbarium there is one specimen of *Parish 2*. All material listed as *No. 22, Parish* (BM, NY) is considered possible type material.

Plants in compact tufts or cushions, greenish-white, becoming whitish-brown with age. Stems 5–15 mm high. Leaves 2–4 mm long, 0.5–0.8 mm broad, closely and densely erect-patent or stiffly patent-spreading, narrowly ovate-lanceolate to lanceolate, shortly acuminate, bluntly acute or rounded obtuse; swollen or fleshy at the apex; margins erect; leaf lamina narrow, consisting of 6–8 rows of long-rectangular, variously porose cells at midleaf and 6–10 rows of elongate-rectangular, firm-walled cells at base; costa with a single dorsal leucocyst-layer and a single ventral leucocyst-layer throughout most of the leaf; ventral leucocysts multi-layered at the extreme apex. Asexual reproduction by brown, multicellular, globose propagula on very short stalks clustered in the leaf axils. Setae smooth, 1.0–1.7 mm long; capsules immersed to emergent, 0.5–0.75 mm long; opercula 1.0 mm long. Calyptrae 4–5 mm long, strongly ciliate at base. Spores spherical, lightly roughened, 10–17 μm.

Distribution. Asia (India, Nepal, Burma, Thailand, and Cambodia).

Illustrations. Bescherelle (1897, figs. 2, 3, 4); Cardot (1900, plate 8, figs. 39, 40); Gangulee (1969, fig. 193); Eddy (1990, fig. 185); FIGS. 13–26.

Habitat. On rotting logs or tree trunks, and soil over rock; 50–1600 m.



FIGS. 13–26. *Ochrobryum kurzianum*. 13. Leaf cross-section at apex. 14 & 15. Leaf apices. 16. Calyptra. 17. Operculum. 18. Capsule, seta and vaginula. 19 & 20. Leaves. 21. Basal leaf lamina. 22. Calyptral hairs. 23 & 24. Globose propagula. 25. Spores. 26. Leaf cross-section at base. Scales in mm: 1 & 2 = 0.1; 3 & 4 = 1.0; 5 & 6 = 0.2. Figs. 13 & 26 from *Touw 9450;* figs. 14–21 from *Kurz 2890;* figs. 22–25 from *Beddome 804*.

Specimens examined. INDIA. Assam: Garo Hills, *Marten 5702* (H, NY); Orissa: Eastern Ghats, Jeypore Talug, *Walker 529, 579* (BM), Russelconda Hills, 19°50′N; 84°35′E, *Beddome 804* (BM, NY). NEPAL. *Wallich 30* (BM). BURMA. Pegu: Pegu-Yomah, *Kurz 2890* (BM, H, NY); Tenasserim: Moulmein, *Parish 2* (BM, NY), *Parish 112* (BM, H), *Stoliczka 4434, 4438* (BM), Martaban, *Kurz 2842* (BM, H, NY). THAILAND. Chanthaburi: Kao Sabah, *Kerr 108* (BM); Kanchanaburi: Ta Kanun, *Kerr 145* (BM); Krabí: Krabí, *Kerr 503* (BM); Payap: 98°35′E, 18°30′N, *Touw 9450* (BM, MO, NY); Trat: Koh Chang, Klong Munsé, *Schmidt 20* (BM, H); Adang: Salut, *Kerr 245* (BM). CAMBODIA. Kandal: near To Bong, *Poilane* (BM, H, NY).

In one paper, Bescherelle (1897) described three *Ochrobryum* species—treated here as one species—based on variations in plant size, leaf apex shape and the number of cell rows in the basal lamina. These distinguishing features are extremely variable and not constantly expressed even within single collections. A nearly identical range of variation is exhibited by *O. gardneri* for the same characters.

Ochrobryum kurzianum and *O. gardneri* were treated by Mitten (1859) as a single species. Bescherelle (1897) separated them on the basis of their allopatric distributions, and the presence in *O. gardneri* of shorter, flatter, narrower, acuminate-acute leaves that had a narrower basal leaf lamina (4 *vs.* 10 rows of cells). Most of these distinctions are not valid, but these two species do differ in three ways. The basal leaf lamina of *O. gardneri* is generally narrower, its propagula are borne on the upper dorsal surface of the leaves rather than in the leaf axils, and its calyptrae tend to be laciniate rather than strongly ciliate at base. The significance of their different geographic distributions is minimized by the occurrence of *O. subulatum* in Asia and South America.

Globose propagula clustered in the leaf axils are also a feature of *O. sessile,* but the two species do not appear closely related. *Ochrobryum sessile* has linear leaves, slenderly acute leaf apices and apical ventral leucocysts that are uni- or bi-layered for only a single cell width.

3. Ochrobryum sakalavum Card. & Par. *in* Card., Bull. Herb. Boissier, Sér. 2, 4: 99. 1904. TYPE. MADAGASCAR. Territoire Sakalave: cercle de Maintirano, secteur de Rakobe, poste d'ampoza, près du village de Tahutofoly, sur bois pourri; récolté par un tirailleur sakalave (PC).

Ochrobryum sakalavum Card. & Par. *in* Par., Rev. Bryol. 29. 1902, *nom. nud.*

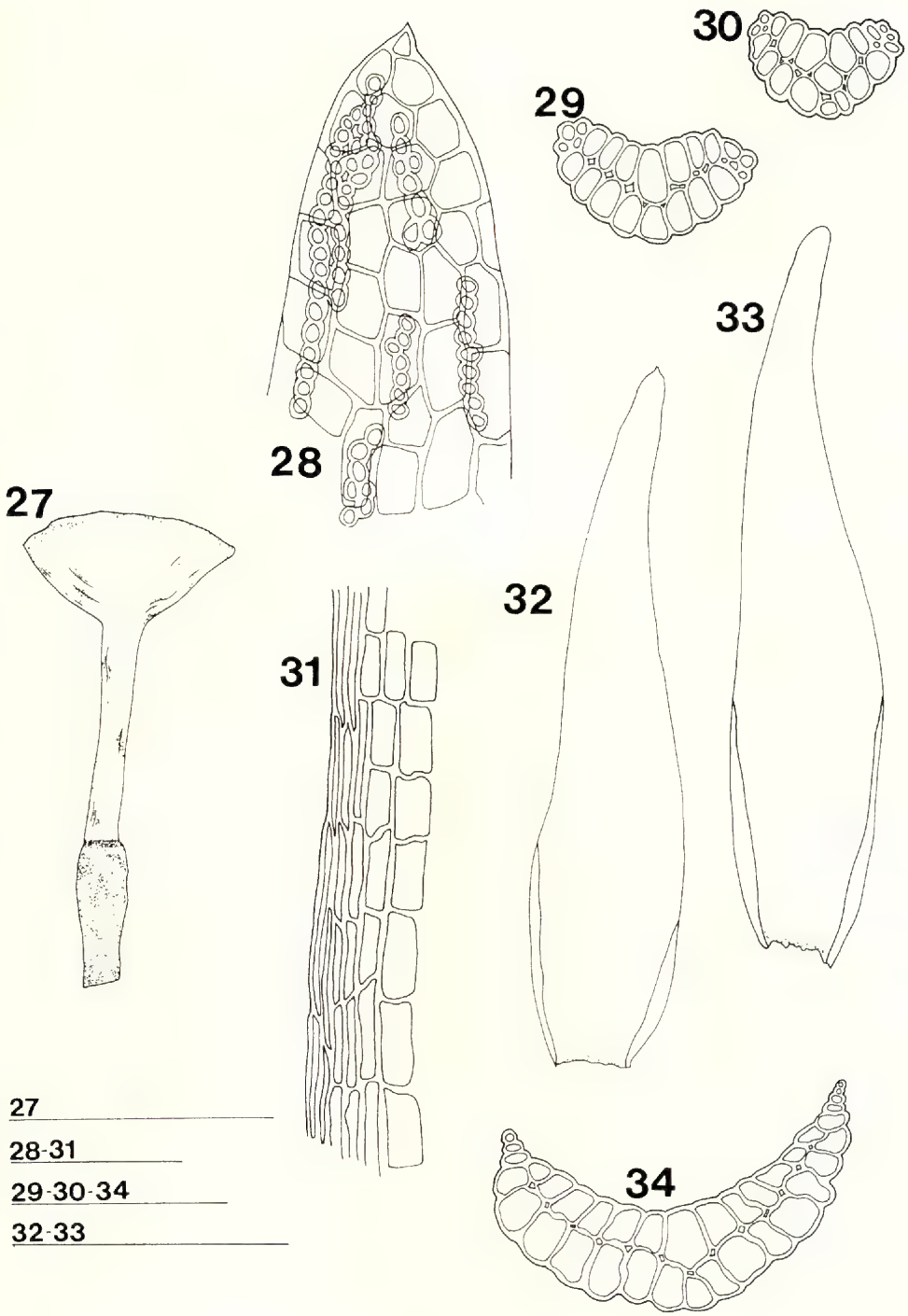
Plants in compact tufts, yellowish-white. Stems 5 mm high. Leaves 2–4 mm long, 0.3–0.4 mm broad, closely erect-patent or subflexuose, narrowly ovate-lanceolate, shortly acuminate, obtuse to subacute and apiculate, not particularly swollen or fleshy at the apex; margins erect; leaf lamina narrow, consisting of 2–4 rows of elongate-rectangular cells at base; costa with a single dorsal leucocyst-layer and a single ventral leucocyst-layer throughout most of the leaf; apical ventral leucocysts in two layers for single cell width at the middle of the leaf. Asexual propagula not seen. Setae smooth, 1.2 mm long (with vaginula); capsules immersed, 0.3–0.5 mm long; operculum and calyptra not seen. [Cardot (1904): operculum convex-conical to 1 mm, calyptra long subulate, fimbriate at base, 2.5–2.75 mm long.]

Distribution. Madagascar.

Illustrations. Renauld and Cardot (1915, pl. 155, figs. 2a–2s); FIGS. 27–34.

Habitat. On rotting wood.

Specimen examined. MADAGASCAR. Territoire Sakalave: cercle de Maintirano, without collector or number (PC).



FIGS. 27–34. *Ochrobryum sakalavum*. 27. Capsule, seta and vaginula. 28. Leaf apex. 29 & 30. Leaf cross section at apex. 31. Basal leaf lamina. 32 & 33. Leaves. 34. Leaf cross-section at base. Scales in mm: 1 & 4 = 1.0; 2 = 0.1; 3 = 0.2. All figures from the type.

Ochrobryum sakalavum has narrowly ovate-lanceolate leaves that are commonly obtuse and apiculate above, narrow leaf laminae, and immersed capsules. This species occupies an intermediate position in the genus. The other four species can be divided into two groups: *gardneri–kurzianum* and *subulatum–sessile*. Its ovate-lanceolate, obtuse, occasionally apiculate leaves are found in the *gardneri–kurzianum* group, but unlike that group the leaf apices are not distinctly fleshy and the apical ventral leucocysts are bi-layered only for a single cell width at the very tip of the leaves. These deviate features are found in the *subulatum–sessile* group, but that group has longer, linear, sharply acute leaves. It differs from all species of *Ochrobryum* by its relatively narrow leaf laminae that are composed of broader, less attenuate cells. Globose propagula were neither reported by Cardot (1904) nor Renauld and Cardot (1915), nor observed in the only collection available for study. This collection had only a few plants and it was not possible to adequately determine if the species produces propagula.

4. Ochrobryum sessile Allen, sp. nov.

Ab *O. gardneri* (C. Müll.) Mitt. cellulis hyalinis distalibus ventralibus saepissime unistratis gemmisque sessilibus in axillis foliorum superiorum differt.

Plants in compact tufts or cushions, dark greenish-white, becoming yellowish-green with age. Stems 3–10 mm high. Leaves 4–5 mm long, 0.2–0.5 mm broad, erect-patent to falcate, narrowly lanceolate, acuminate, ending in a single sharp, hyaline cell, flattened above and commonly spirally twisted when dry; margins erect to incurved below; leaf laminae narrow, consisting of 2–3 rows of long-rectangular, variously porose cells at midleaf and 4–5 rows of elongate-rectangular cells at base; costa with a single dorsal leucocyst-layer and a single ventral leucocyst-layer throughout most of the leaf, apical ventral leucocysts occasionally two-layered for a single cell width. Asexual reproduction by hyaline or brown, multicellular, globose propagula on short or long stalks usually clustered in the axils of the upper leaves, at times also in the lower leaf axils or on slender rhizoids at base of stem. Setae smooth, 1.0–1.5 mm long; capsules immersed to emergent, 0.7–1.0 mm long; opercula 1.5–2.0 mm long. Calyptrae 3–6 mm long, weakly ciliate at base. Spores spherical, lightly papillose, 15–18 μm.

Type. Colombia. Meta: in *Remijia* forest west of Cordillera Oriental, *Steere 7654* (MO holotype; H, NY isotypes).

Distribution. Central and South America (Costa Rica, Panama, Colombia, and Venezuela).

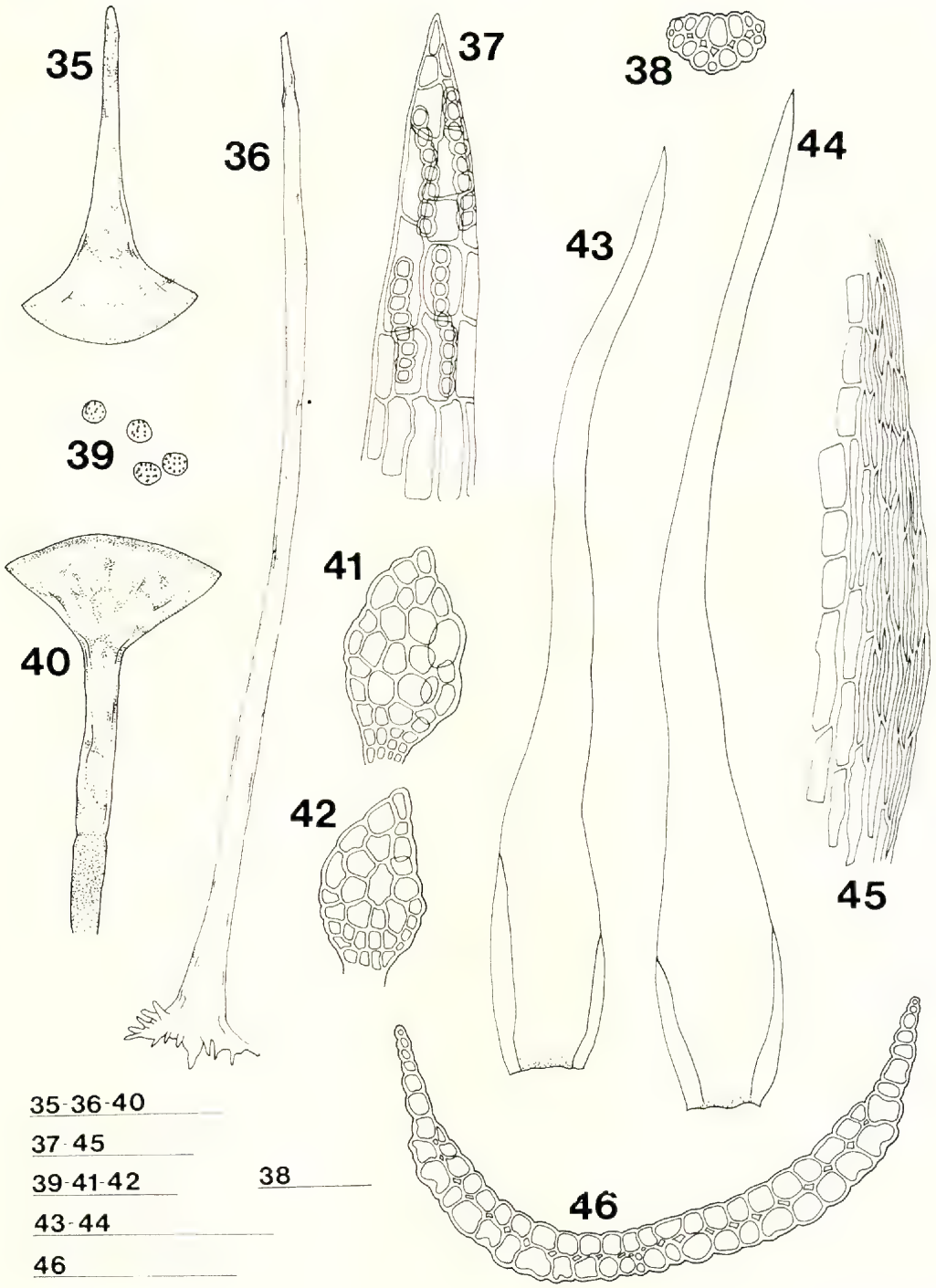
Illustrations. Figs. 35–46.

Habitat. On rotting logs or bark at base of trees; 700–2000 m.

Specimens examined. CENTRAL AMERICA. Costa Rica. San José: El General, *Skutch 2209* (FH, MO, US); Puntarenas: 5 km S of S. Vito, *Crosby 2658* (MO). Panama. Darién: Pirre Massif, W of Cana, *Allen 8849, 8891* (MO, PMA); Panamá: Cerro Azul, *Castillo 112C* (MO).

SOUTH AMERICA. Colombia. Meta: Remija west of Villavicencio, *Steere 7654* (H, MO, NY). Venezuela. Aragua: Parque Nacional Henri Pittier, *Guzmán Ma-761a* (US); Carabobo: between Valencia and Maracay, *Alston 6152* (BM, FH, US).

This species resembles *O. subulatum* in leaf shape, but is a larger plant that grades into the more narrow-leafed expressions of *O. gardneri*. It differs from *O. subulatum* not only by its larger, more frequently spirally twisted leaves but also by its more strongly papillose spores, and propagula clustered in the leaf axils—a



FIGS. 35–46. *Ochrobryum sessile*. 35. Operculum. 36. Calyptra. 37. Leaf apex. 38. Leaf cross-section at apex. 39. Spores. 40. Capsule, seta and vaginula. 41 & 42. Globose propagula. 43 & 44. Leaves. 45. Basal leaf lamina. 46. Leaf cross-section at base. Scales in mm: 1 & 4 = 1.0; 2, 3 & 6 = 0.1; 5 = 0.2. All figures from the type.

feature it shares with *O. kurzianum*. In *O. gardneri* and *O. kurzianum* the leaf tips are thickened, fleshy and have an extensive multi-layered ventral leucocyst pattern. In addition, *O. gardneri* has propagula borne on the upper dorsal surface of the leaves. The leaf tips in *O. sessile* are identical to those of *O. sakalavum* in having the apical ventral leucocysts two-layered for a single cell width at the middle of the leaf. *Ochrobryum sakalavum* has obtuse leaf tips.

5. Ochrobryum subulatum Hampe *in* Besch., J. Bot. (Morot) 11: 150. 1897. TYPE. BURMA. Plumadoe, *Kurz 2833* (BM holotype; H, NY isotypes).

Ochrobryum subulatum Hampe *in* F. Mason, Burma 2: 49. 1883, *nom. nud.*

Ochrobryum stenophyllum Besch., J. Bot. (Morot) 11: 150. 1897. TYPE. BRAZIL. *Spruce 73 p.p.* (BM holotype; BR isotype; *Spruce 73b* BM, H isotypes), see nomenclatural note 2, *syn. nov.*

Ochrobryum maclaudii Card. & Par. *in* Par., Rev. Bryol. 30: 101. 1903. TYPE. GUINEA. Ad ligna semiputrida secus amnem Féfiné, 20 mart. 1903, *Maclaud* (H, NY isotypes), see nomenclatural note 3, *syn. nov.*

Ochrobryum normandii var. *fragilifolium* Dix. & Thér., Rev. Bryol. Lichénol. 12: 69. 1942. TYPE. ZAIRE. Lulua, octob. 1923, *Overlaet* (BM isotype), *syn. nov.*

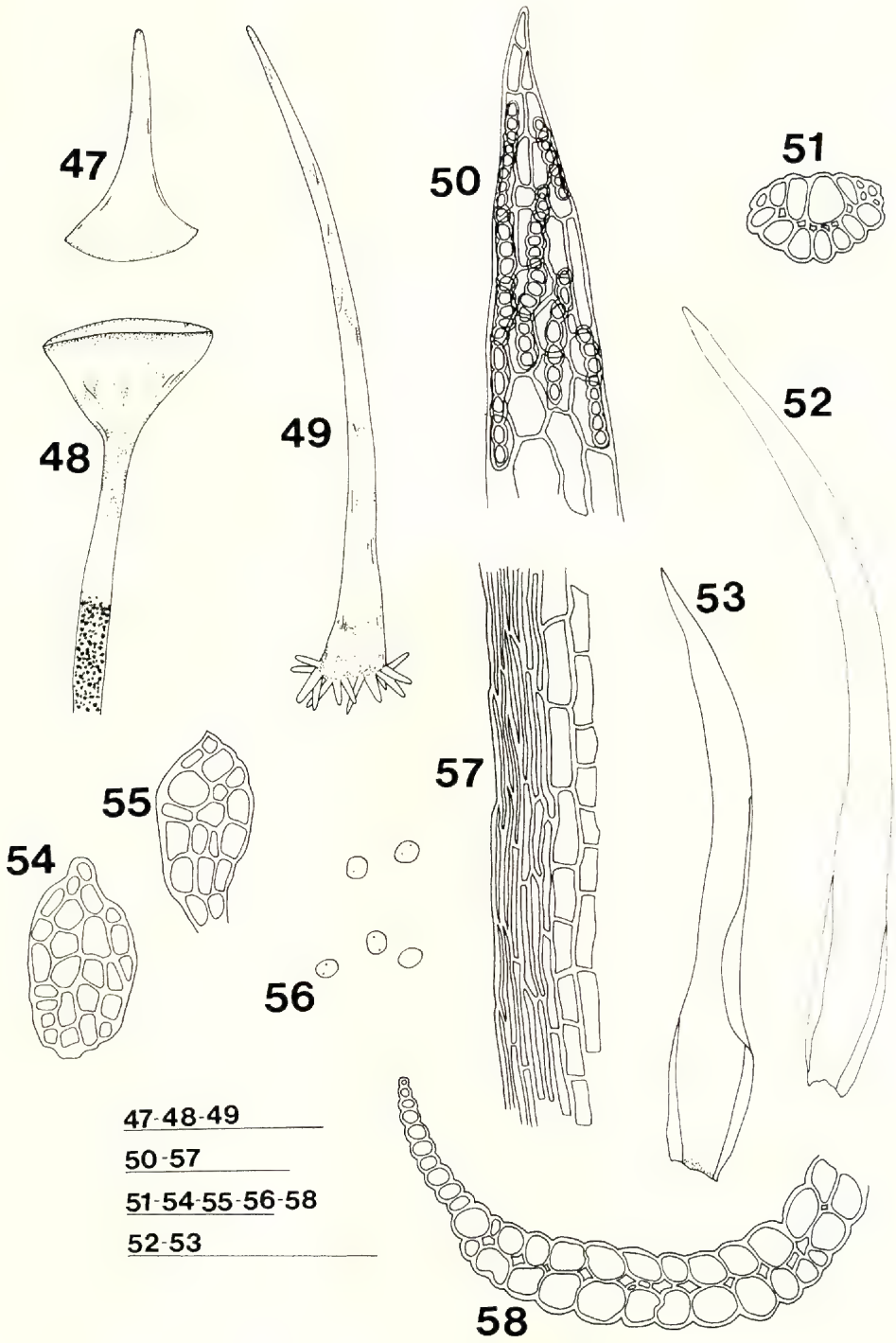
Ochrobryum microphyllum Card. *ex* Herz., Hedwigia 61: 295. 1919, *nom. illeg.*, see nomenclatural note 4. Based on MALAYSIA. Malakka obes "Batang Padang-Tal", *Stresemann 86* (H). Non *O. microphyllum* (Besch.) Card.

Ochrobryum herzogianum Mohamed & Tan, Bryologist 91: 29. 1988, *nom. nov.* for *O. microphyllum* Card. *ex* Herz., *nom. illeg.*

Nomenclatural notes.

1. *Ochrobryum subulatum* and *O. stenophyllum* have equal priority. The epithet *subulatum* was chosen for the combined species because its type material is better.
2. The type of *O. stenophyllum* was separated from a specimen in PC (*Spruce 73*) issued by Spruce in his Musci Amazonici et Andini exsiccati. Previously, *Spruce 73* in BM had been recognized as a mixed collection, divided, and given the numbers *Spruce 73* and *Spruce 73b*. *Spruce 73b* (BM) is identical to the holotype of *O. stenophyllum*. *Spruce 73* (BM) is identical to the holotype of *O. gardneri* var. *microphyllum*.
3. Cardot and Paris failed to cite type material for *Ochrobryum maclaudii*. The type was later designated by Paris (1904).
4. *Ochrobryum microphyllum* Card. *ex* Herz. was never validly described, furthermore neither Herzog (1919) nor Dixon (1926) intented to describe a new species for this taxon. Likewise *O. herzogianum* is also invalid. The specimen on which the name is based is *O. subulatum*.

Plants slender, in compact or loose tufts. Stems 2–4(–7) mm long. Leaves 2.0–4.5 mm long, erect-patent to secund, linear, evenly tapered from the base to a setaceous or narrowly acuminate apex, not apiculate, but frequently ending in a single, sharp, clear cell; margins erect below; leaf lamina restricted to 5–6 rows of linear or elongate-rectangular cells at basal margins; costa in cross-section with a single ventral leucocyst-layer and a single dorsal leucocyst-layer throughout the leaf. Vegetative reproduction by globose, multicellular propagula arising on short stalks and occurring in terminal clusters on specialized branches or stem extensions; propaguliferous branches to 2 mm long, red-brown, with short, ovate leaves. Setae 1.0 mm long; capsules hemispherical to cupulate, 0.5 mm long; opercula 1.5 mm long. Calyptrae 3–4 mm long, ciliate at base. Spores smooth to lightly roughened, 17–20 μm.



FIGS. 47–58. *Ochrobryum subulatum*. 47. Operculum. 48. Capsule, seta and vaginula. 49. Calyptra. 50. Leaf apex. 51. Leaf cross-section at apex. 52 & 53. Leaves. 54 & 55. Globose propagula. 56. Spores. 57. Basal leaf lamina. 58. Leaf cross-section at base. Scales in mm: 1 & 4 = 1.0; 2 & 3 = 0.1. Figs. 47–49, 51, 58 from *Touw 10290;* figs. 50, 52, 53, 57 from *Kurz 2883;* figs. 54–56 from *Fife et al. 4247.*

Distribution. Asia (Burma, Thailand, and Malaysia); South America (Venezuela, Brazil, and Bolivia); Africa (Guinea and Zaire).

Illustrations. Bescherelle (1897, fig. 7); Cardot (1900, pl. 8, figs. 38, 42); FIGS. 47–58.

Habitat. On rotting, decorticated logs and on bark at base of trees; 100–1650 m.

Specimens examined. ASIA. BURMA. Plumadoe, *Kurz 2833* (BM, H, NY). THAILAND. 18°35′N, 98°30′E, *Touw 10290* (BM, MO, NY). MALAYSIA. Batang Padang-Tal, *Stresemann 86* (H).

SOUTH AMERICA. VENEZUELA. Bolívar: 4°25′N, 61°20′W, *Steyermark & Dunsterville 112253* (MO); Mérida: 7°41′N, 71°28′W, *Liesner & Gonzáles 9371* (MO). BRAZIL. Acre: 33 km S of Rio Branco along road to Brasiléia, *Reese & McPherson 13263* (MO, NY); Alagoas: 33 km N of Maceió, *Boom & Mori 1024* (NY); Goiás: 3 km S of São João de Aliança, *Irwin et al. 31982 p.p.* (FH, H, NY); Mato Grosso: Veu de Noiva, Chapada dos Guimarães, *Prance et al. 19015, 19016, 19149, 19398* (all NY); Minas Gerais: near Franca, *Wacket 1171, 1172* (H); Rondônia: 11°S, 64°W, *Reese 13488* (MO, NY, US), 15 km E of Santa Barbara, *Prance & Ramos 6910* (FH, NY), 9°10′S, 63°07′W, *Fife et al. 4247* (MO), 128 km SW of Ariquaes, *McFarland 138* (MO, NY). BOLIVIA. Beni: vicinity of Guayaramerín, *Reese 12910, 13130* (MO, NY).

AFRICA. GUINEA. Koulaire, *Maclaud* (H), Casamonce-Boubounda, *Maclaud* (H), along Féfiné River, *Maclaud* (H, NY). ZAIRE. Lulua, *Overlaet* (BM).

This is the smallest species in the genus and the only one with propagula in terminal clusters on specialized branches or stem extensions. The propaguliferous branches can be recognized, even without propagula, by their terminal position, striking red-brown color and short, ovate leaves.

Ochrobryum subulatum and *O. sessile* form a pair united by their narrow leaves that smoothly taper from base to a setaceous or long-acuminate apex. Unlike *O. kurzianum, O. gardneri,* and *O. sakalavum* the apex is not obtuse or apiculate. However, the leaves frequently end in a single, sharp, clear cell, a condition also seen in *O. sessile* and some leaves of *O. gardneri. Ochrobryum kurzianum* and *O. gardneri* also have thickened or swollen leaf apices. *Ochrobryum sessile* is a larger plant with falcate leaves that are distinctly twisted when dry. It has propagula clustered in the leaf axils and calyptrae that are weakly ciliate at base.

In South America and Africa *O. subulatum* often occurs mixed with *O. gardneri. Ochrobryum gardneri* has larger, stouter leaves, some obtuse, swollen leaf apices, and leaf propagula on the upper dorsal surface of the leaves.

There is a small, sterile *Leucobryum*-like moss in Brazil (*Buck 2336* NY, *2749* NY, *3081* MO, NY) that closely mimics *O. subulatum* in size and aspect. This taxon also has leaves with a single layer of dorsal and ventral leucocysts. It differs from *O. subulatum* in its virtual absence of a basal leaf lamina, lack of globose propagula and the presence of rectangular chlorocysts in the upper parts of its leaves.

TYPES NOT SEEN

Ochrobryum mittenii C. Müll. *ex* Besch., J. Bot. (Morot) 11: 148. 1897. TYPE. CEYLON. 1862, *Nietner* (in Herb. C. Müll.).

Ochrobryum nietneri C. Müll. *ex* Besch., J. Bot. (Morot) 11: 151. 1897. TYPE. CEYLON. 1862, *Nietner* (in Herb. C. Müll.).

Cardot (1900) provisionally excluded these species from *Ochrobryum* since their sporophytes were unknown. From their descriptions it is not possible to determine if they belong in *Ochrobryum.*

EXCLUDED SPECIES

Leucobryum incurvifolium C. Müll.

Ochrobryum obtusissimum Dix., J. Bot. 76: 225. 1938. TYPES. TANZANIA. Mufindi, *Balbo 96* (BM holotype); NYASALAND [MALAWI]. Bandowe, Chinteche, *Little 2539* (BM paratype), Nchese Mt., *Davy 1312* (BM paratype), *syn. nov.*

The sporophytes of *O. obtusissimum* are unknown, but the presence of multilayered leucocysts in the leaf bases, quadrate lower laminal cells and masses of brood leaves at the stem apices are features indicative of *Leucobryum* rather than *Ochrobryum*. In these gametophytic features, as well as its leaf shape, cucullate, fleshy leaf apices, and rounded apical chlorocysts it is a perfect match for *Leucobryum incurvifolium*. The inclusion of this taxon in *L. incurvifolium* gives that species a bi-centric distribution: Central America (Mexico to Honduras, see Robinson 1965, and Nicaragua [*Standley 9561*, F, FH])—Africa (Angola [*Gossweiler 11448*, BM], Malawi, Tanzania).

Leucobryum subobtusifolium (Broth.) Allen, *comb. nov.*

Ochrobryum subobtusifolium Broth., Bih. Kongl. Svenska Vetensk.-Akad. Handl. 26 Afd. 3(7): 10. 1900. TYPE. BRAZIL. Mato Grosso: Serra da Chapada, *Lindman 402* (H holotype; H isotype).

Ochrobryum parvulum Besch., J. Bot. (Morot) 11: 147. 1897. Non *Leucobryum parvulum* Card. TYPE. BRAZIL. Ad flumen Amazone, *Spruce 73 p.p.* (BR isotype), *syn. nov.*

Ochrobryum gardneri var. *microphyllum* Besch., J. Bot. (Morot) 11: 142. 1897. *Ochrobryum microphyllum* (Besch.) Card., Mém. Soc. Sci. Nat. Cherbourg 32: 28. 1900. TYPE. BRAZIL. Sur les troncs d'arbres le long du fleuve Amazone, *Spruce 73 p.p.* (BM holotype; BR isotype) *syn. nov.*

The oldest name for this taxon in *Leucobryum* is preoccupied by *L. parvulum* Card. The epithets *subobtusifolium* and *microphyllum* have the same year of priority (both distributed as off-prints at earlier dates than the journals in which they appeared). *Ochrobryum subobtusifolium* appeared sometime between 14 March and 31 December 1900; *O. microphyllum* sometime between 31 May and 31 December 1900. I have not determined the exact dates of issue for these off-prints but have chosen the epithet *subobtusifolium* as the name for the combined species because of its potentially earlier date.

The sporophytes of this species are unknown and so its generic position is uncertain. Unlike *Ochrobryum* it reproduces asexually by means of apical clusters of brood leaves rather than globose propagula. It is similar to *Leucobryum incurvifolium* and like that species and *Ochrobryum* species has short, rounded apical leaf chlorocysts. It differs from *L. incurvifolium* in having its dorsal and ventral leucocysts in a single layer throughout the leaf.

Leucobryum ceylanicum (Besch.) Card., Mém. Soc. Sci. Nat. Cherbourg 32: 15. 1900. *Ochrobryum ceylanicum* Besch., J. Bot. (Morot) 11: 148. 1897. TYPE. CEYLON. *Thwaites 81* (BM holotype; H, NY isotypes).

The sporophytes of this species are unknown. Cardot (1900) transferred it to *Leucobryum* on the basis of its multilayered, basal leucocysts.

Leucobryum humillimum Card., Mém. Soc. Sci. Nat. Cherbourg 32: 15. 1900, *nom. nov. pro Ochrobryum wightii* Besch., J. Bot. (Morot) 11: 149. 1897, non *Leucobryum wightii* Mitt. TYPE. INDIA. Madras, *Wight* (BM holotype; BM, NY isotypes).

Ochrobryum propaguliferum Dix., Notes Roy. Bot. Gard. Edinburgh 19: 281. 1938. *Leucobryum propaguliferum* (Dix.) Robins., Bryologist 68: 91. 1965. TYPE. CEYLON [SRI LANKA]. Hunasgiriya, *Alston 1895* (BM holotype). PARATYPES. CEYLON [SRI LANKA]. Hatton near Hambantotuoya, *Alston 2607* (BM); *Wight* (E, not seen), *syn. nov.*

Dixon unwittingly suggested the above synonymy by his inclusion of an isotype of *O. wightii* in the protologue of *Ochrobryum propaguliferum*. Robinson (1965) placed *O. propaguliferum* in *Leucobryum* on the basis of its terminal clusters of deciduous leaves. As in *Ochrobryum* this species has a single layer of dorsal and ventral leucocysts throughout the leaf.

ACKNOWLEDGMENTS

I thank BM, BR, H, F, FH, NY, PC and US for the loan of material. I am especially grateful to Gordon McPherson for help with French translation.

LITERATURE CITED

Andrews, A. L. 1947. Taxonomic notes VI. The Leucobryaceae. Bryologist 50: 319–326.

Bartram, E. B. 1949. Mosses of Guatemala. Fieldiana, Bot. 25: i–v, 1–442.

Bescherelle, É. 1897. Révision du genre *Ochrobryum*. J. Bot. (Morot) 11: 138–153.

Cardot, J. 1900–1902 [1900]. Recherches anatomiques sur les Leucobryacées. Mém. Soc. Sci. Nat. Cherbourg 32: 1–84.

———. 1904. Les Leucobryacées de Madagascar et des autres Îles Austro-Africaines de L'Océan Indien. Bull. Herb. Boissier, Sér. 2, 4: 97–118.

Dixon, H. N. 1926. A list of the mosses of the Malay peninsula. Gard. Bull. Straits Settlem. 4: 1–46.

Eddy, A. [1990]. *A Handbook of Malesian Mosses. Vol. 2. Leucobryaceae to Buxbaumiaceae*. Natural History Museum Publications, London.

Gangulee, H. C. 1969. *Mosses of Eastern India and Adjacent Regions. Fascicle 1. Sphagnidae, Andreaidae & Nematodonteae*. Calcutta, India.

Geheeb, A. 1901. Révision des mousses récoltées en Brésil dans la province de San-Paulo par M. Juan J. Puiggari pendant les années 1877–1882. Rev. Bryol. 28: 9–11.

Greuter, W. (ed.). 1988. International code of botanical nomenclature. Regnum Veg. 118: i–xiv, 1–328.

Herzog, T. 1919. Die Laubmoose der zweiten Freiburger Molukkenexpedition. Hedwigia 61: 286–299.

Lindberg, S. O. 1872. Contributo ad floram cryptogamam Asiae Boreali-Orientalis. Acta Soc. Sci. Fenn. 10: 223–280.

Mitten, W. 1856. A list of some mosses and Hepaticae, collected by the Rev. Charles Parish at Moulmein, and communicated to Sir W. J. Hooker. Hooker's J. Bot. Kew Gard. Misc. 8: 353–357.

———. 1859. Musci Indiae Orientalis: an enumeration of the mosses of the East Indies. J. Proc. Linn. Soc., Bot. Suppl. 1: 1–171.

———. 1869. Musci Austro-Americani. J. Linn. Soc., Bot. 12: 1–659.

Müller, C. 1849. *Synopsis Muscorum Frondosorum. 1*. Foerstner, Berlin.

Paris, [E. G.]. 1904. *Ochrobryum maclaudii* et *normandi*. Rev. Bryol. 31: 14.

Renauld, F. and J. Cardot. 1915. Mousses. *In:* A. & G. Grandidier (eds.), *Histoire, physique, naturelle et politique de Madagascar* 39: 1–526.

Robinson, H. 1965. Notes on Leucobryaceae in Central America. Bryologist 68: 89–93.

———. 1990. A functional evolution of the Leucobryaceae. Trop. Bryol. 2: 223–237.

Wijk, R. van der, W. D. Margadant and P. A. Florschütz. 1964. Index Muscorum Vol. III (*Hypnum*–O). Regnum Veg. 33: 1–529.

Yano, O. 1975. *Leucobryaceae (Musci) do Estado de São Paulo*. M.S. Dissertation, Área de Productos Naturais, Escola Paulista de Medicina, São Paulo, Brazil.

Contr. Univ. Mich. Herb. 18:131–140. 1992.

REPRODUCTIVE BIOLOGY OF THE RARE "COPPER MOSS" MIELICHHOFERIA MIELICHHOFERIANA

A. Jonathan Shaw, N. J. Niguidula and T. M. Wilson
Department of Biology
Ithaca College
Ithaca, NY 14850, U.S.A.

INTRODUCTION

The "copper mosses" are unique among land plants. These plants, which actually include both mosses and liverworts, have extremely broad geographic ranges that typically span several continents. Broad intercontinental distributions are not, of course, especially remarkable for bryophytes, as most species of mosses and liverworts have wide ranges compared to seed plants. It is the highly restricted and disjunct occurrences with each site hundreds or even thousands of miles from the nearest station, a general rarity of sexual reproduction over much of their ranges, and at least some association with deposits of copper and/or other metals, that sets the copper mosses apart from other plants. The fact that several species of copper moss often co-occur at precisely the same widely separated stations makes their geographic distributions and ecological characteristics unique and even more bizarre.

There are different kinds of rare plant species, each with different biological causes. Rarity resulting from habitat specificity is one of three basic types recognized by Rabinowitz (1981) and others interested in explaining the biological basis of rarity. These species are thought to be sporadic in occurrence primarily because their habitats are discontinuous and uncommon. Rarity resulting from edaphic specificity has been most thoroughly studied with regard to serpentine endemism (Kruckeberg 1984), but species restricted to deposits enriched with heavy metals such as copper and zinc are also known (Antonovics *et al.* 1971). Some highly restricted taxa are endemic to deposits at one or a few metal mines and appear to have originated *in situ* from widespread, more ecologically generalized species. For example, *Mimulus cupriphilus* Macnair (Macnair 1989) is known only from two copper mines in the foothills of the Sierra Nevada Mountains of California and appears to be a derivative of the widespread species, *Mimulus guttatus* Fischer *ex* DC. Perhaps a comparable example among the mosses is *Ditrichum plumbicola* Crundw., described from lead mine wastes in Great Britain and clearly related to the more widespread species, *D. lineare* Sw. (Crundwell 1976). Species known as copper mosses, however, are very different biogeographically and ecologically from these narrow endemics, and certainly represent a different form of rarity reflecting different ecological limitations and evolutionary histories. The widely distributed, disjunctive copper mosses pose biological questions that are without parallel in any other plant group.

The copper mosses themselves are ecologically and taxonomically heterogeneous. They include about ten species of mosses and liverworts representing eight families. For most species the relationship with copper appears to be facultative, and typical substrate copper levels vary from one species to another (Shaw 1990). *Mielichhoferia mielichhoferiana* (Funck) Loeske was one of the first plants to be

recognized as a copper moss. The species was described on the basis of collections made by Malthias Mielichhofer in 1815 on copper mine tailings in the Salzburg area of what is now Austria, and numerous subsequent authors have reported a correlation between occurrences of *M. mielichhoferiana* and copper deposits (reviews in Persson 1956; Shacklette 1967; Shaw 1990). The genus *Mielichhoferia* is comprised of about 25 species in South America, Africa, and some of the Pacific Islands, and is represented by 3–4 species in North America and northern Eurasia. *Mielichhoferia mielichhoferiana,* with scattered occurrences across North America, Europe, and Asia (south to Japan), is the most widespread of the northern taxa. In contrast, *M. tehamensis* Showers is found only around Mt. Lassen, a volcanic peak in north-central California, and *M. macrocarpa* (Hook. *ex* Drumm.) Bruch & Schimp. *ex* Jaeg. is known from about ten disjunct sites in Canada and the United States and at one extremely isolated site in central Asia.

Research described in this paper deals with certain factors that might control the distribution and abundance of *Mielichhoferia mielichhoferiana.* The species is exceedingly rare throughout its range. For example, in the northeastern United States, it has been found at only one site each in Maine and Michigan, and at two sites separated by over 300 km in New York. From these sites in the northeastern and north-central United States, the species is disjunct at about five proximate localities (i.e., within a few km) in the southern Appalachian Mountains along the border of Tennessee and North Carolina (Schofield 1959). Additional disjunct populations occur in the western United States, boreal and arctic Canada, and Alaska.

It has not been demonstrated that the presence of higher than normal concentrations of copper is the critical factor limiting the abundance of *M. mielichhoferiana* (or, in fact, any other copper moss). Although substrate copper concentrations reported in the literature for this species tend to be elevated relative to most soils (Persson 1956; Shacklette 1967; Shaw 1990), a considerable number of populations grow on soils or rocks with only trace amounts of copper (Shaw 1990, unpublished data). The species may show an association with sulfur (Schatz 1955) rather than copper (most copper deposits also contain high sulfur), but little data on substrate sulfur concentrations are available. Substrates of *M. mielichhoferiana* are exceptionally acidic and this ecological characteristic is in fact more consistent across the range of the species than is enrichment with copper: 21 North American soils samples had the remarkably low mean pH of 3.6 (unpublished data). Experimental studies of mineral nutrition in *M. mielichhoferiana* will be reported in a later paper.

This paper reports studies on the reproductive biology of *M. mielichhoferiana.* Previous discussions of factors limiting the distribution and abundance of copper mosses have focussed on substrate chemistry, but the rarity of spore formation suggests that these species may have limited potential for dispersal and establishment of plants in nature. Virtually nothing is known about reproductive processes in natural populations of the copper mosses. It has been suggested that plants rare because of extreme habitat specificity might be genetically uniform (Huenneke 1991). This uniformity could result from founder events and population bottlenecks that occur during colonization of disjunct localities, and inbreeding due to small population sizes. This might be especially true of the copper mosses such as *M. mielichhoferiana,* in which sexual reproduction appears to occur infrequently. A series of questions were addressed in this study. What factor(s) limit sporophyte formation in natural populations? When sporophytes are formed, do they contain viable spores? How do germination percentages vary among sporophytes and populations? Do germinating spores produce viable gametophytes? Do populations dif-

fer in gametophytic growth rates? Are gametophytic plants capable of vegetative regeneration following prolonged dormancy and does this capability vary among populations?

MATERIALS AND METHODS

Plants from widely disjunct populations were included in the experimental work (FIG. 1). These five populations represent five states spanning a range from the Atlantic to the Pacific coasts of the United States. In **New York,** *M. mielichhoferiana* grows on moist, somewhat crumbly metamorphic rock along Cattaraugus Creek and several of its tributaries in Cattaraugus and Erie Co. (no. 1 in FIG. 1). The species occurs at several localities within a few kilometers of each other. Copper occurs at trace concentrations only at these sites. Collections of *M. mielichhoferiana* were originally made from Cattaraugus Creek in 1941. It presently

FIG. 1. North American map showing the distribution of collections used in the experimental studies on *Mielichhoferia mielichhoferiana* described in this paper.

occurs as numerous colonies of varying sizes on vertical or nearly vertical rock. The only **Michigan** population of *M. mielichhoferiana* (FIG. 1, no. 2) grows on moist rocks along the south shore of Lake Superior in Pictured Rocks National Lakeshore. Professor G. E. Nichols collected *M. mielichhoferiana* there originally in August, 1933, the first record for this species in North America (Andrews 1933). Numerous collections of *M. mielichhoferiana* have been made subsequently from Pictured Rocks, but the population has never been marked and it is not clear to what extent all collections derive from precisely the same population. The present collection, made during October, 1990, originated at a north-facing site subject to harsh winds and severe weather from Lake Superior. Field work at several of the other accessible areas along Lake Superior did not reveal additional sites for the species. Shacklette (1967) reported elevated copper levels in substrates of *M. mielichhoferiana* from Pictured Rocks. In fact, the Upper Peninsula of Michigan is famous for extensive copper deposites that have been mined for hundreds of years.

In **Tennessee** (FIG. 1, no. 3; actually on the North Carolina border), *M. mielichhoferiana* occurs at several sites within a few kilometers of each other in the Great Smoky Mountain National Park (Schofield 1959). The experimental population grows at "Charlie's Bunyan", a large outcrop of schist amidst a mixed hardwood-conifer forest at approximately 5000 ft. elevation. The moss is abundant in protected recesses on the rock.

In **Colorado,** *M. mielichhoferiana* occurs at scattered localities and has been found at a number of abandoned mines in Ouray Co. At one mine, *M. mielichhoferiana* occurs with *M. macrocarpa.* The site is one of only three areas that *M. macrocarpa* has been found in the United States outside of Alaska. The experimental population grew on mine tailings at approximately 10,000 ft elevation just north of the summit of Red Mountain Pass (FIG. 1, no. 4). The last experimental population, from **California** (FIG. 1, no. 5), occurred on decomposing metamorphic rock along a roadside in the Sierra Nevada Mountains. The moss is abundant at the site, but only over a distance of about 25 meters along the road. Field work did not reveal any additional sites in the area.

The reproductive behavior of gametophytic plants was investigated by intensively sampling individuals from the New York population. Preliminary work showed that plants form gametangia in the spring and sporophytes mature in late summer and autumn. During June of 1990, 317 plants were collected and scored for the presence of archegonia or antheridia. Plants occurred on the gorge walls as discrete colonies that were sampled independently in order to assess small scale between-colony differences in reproductive behavior. This sampling scheme was repeated in 1991, when a total of 419 plants were collected. During the second year of sampling, the sizes of individual colonies were estimated in order to determine if there was a relationship between colony size and sexual expression. For each colony, the longest two dimensions were measured in centimeters.

Spore germination percentages were estimated for 30 sporophytes from the Michigan population, and ten each from the New York and California populations in the following manner. Sporophytes were surface sterilized by soaking in full strength bleach for 8 minutes, rinsed in sterile distilled water, and the spore contents were emptied into 4 ml of distilled water. 0.5 ml of the spore suspension was then pipetted onto a Knopp's nutrient medium (recipe in Basile and Basile 1988) solidified with 1.2% agar. Three replicate cultures were initiated from each sporophyte and the petri dishes were completely randomized on a lighted shelf with a 14 hour photoperiod.

Another experiment was initiated to determine if germinating spores produce vigorous sporelings, and whether sporeling vigor varies among natural populations. Spores from five sporophytes each from the Michigan, New York, Tennessee, and California populations were inoculated on Knopp's medium. Only one sporophyte was included from the Colorado population because no others were available. Two days after the spores germinated, the lengths of ten randomly selected sporelings were measured under a compound microscope. Three replicate cultures of each sporophyte were inoculated and the dishes were completely randomized as in the previous experiment.

The viability of gametophytes following a prolonged period of dormancy was assessed by incubating stem fragments in liquid Knopp's medium. Gametophytic plants were collected from a series of Colorado populations during the summer of 1990. These plants were then stored as herbarium specimens until the spring of 1991. In April, 1991, 25 stems from each population were placed in Knopp's medium in 5 ml sterile tissue culture tubes (one stem per tube). After one month, the presence or absence of renewed gametophytic growth was scored in each tube. This growth was most commonly in the form of elongation and branching of the original fragment. In some cases, protonemata and/or rhizoids were also produced. A second and third replicate block of 25 stems from each population were initiated during the spring and summer of 1991, and each was scored in a similar manner following one month of incubation in Knopp's medium.

RESULTS AND DISCUSSION

Few sporophytes were observed in the New York population during the 1990 and 1991 seasons. This is consistent with observations made on populations elsewhere in the United States during the last three years in which relatively few sporophytes were observed (unpublished data), and with literature reports in which absence or scarcity of sporophytes has been noted (e.g., Hartman 1969; Schofield 1959). Repeated visits to a population in Colorado showed that successful sporophyte formation varies tremendously from year to year (Hartman 1969). The population at Pictured Rocks, Michigan, on the other hand, has been visited repeatedly since it was discovered in 1933, and numerous herbarium specimens have been collected with abundant sporophytes over the years. Without yearly visits and systematic sampling of populations, however, it is impossible to determine what factors limit sporophyte formation during any given year.

At the New York site, over 90% of the plants collected during both the 1990 and 1991 seasons lacked gametangia of either sex (Table 1). In 1990, only six out of 317 plants bore antheridia, and only 20 bore archegonia. In 1991, the percentage of sterile plants was exactly the same as in the previous year (92%), but the proportions of plants bearing archegonia versus antheridia was reversed (Table 1). Since the combined abundance of reproductive plants was so low in both years, the difference between male and female reproductive expression in 1990 and 1991 may well be the result of sampling error. On the other hand, the scarcity of reproductive plants in general is clearly at least a proximate cause for the rarity of sporophytes in this population.

Successful sporophyte formation is dependent not only on the formation of archegonia and antheridia, but on their proximity, since gamete dispersal is limited by the ability of free-swimming sperm to reach eggs. Plants of *M. mielichhoferiana*

TABLE 1. Sexual expression in gametophytes from the Cattaraugas Co., New York population of *Mielichhoferia mielichhoferiana*.

	1990	1991
Total Plants	317	419
Male Plants	6 (2%)	27 (6%)
Female Plants	20 (6%)	7 (2%)
Sterile Plants	291 (92%)	385 (92%)
Total Colonies	18	45
Male Colonies	4 (22%)	12 (27%)
Female Colonies	4 (22%)	0
Bisexual Colonies	1 (6%)	1 (2.2%)
Sterile Colonies	9 (50%)	32 (71%)

at the New York site occur in more or less discrete colonies, and when these are separated by more than a few centimeters it is likely that successful fertilization will occur primarily or exclusively between plants within individual colonies. During both 1990 and 1991, only one colony each year was observed with both male and female reproductive plants (TABLE 1). It is not surprising that these colonies were the only ones that bore sporophytes each year. Approximately one fourth of the colonies sampled each year bore male but no female gametangia. During 1990, four colonies contained female but no male gametangia, but in 1991 no such exclusively female colonies were sampled (TABLE 1). The total number of fertile colonies was too low to determine if there was a relationship between colony size and sexual expression. In 1990, the only colony with both males and females was among the smallest (< 25 cm^2). In 1991, the bisexual colony was by far the largest, occupying several meters^2 of the rock wall.

Studies of the factors limiting sporophyte formation in moss populations have shown that plants bearing antheridia are often scarce in spite of an abundance of plants with archegonia (review in Longton & Schuster 1983). In some dioicous mosses, spatial separation of male and female plants may severely limit fertilization frequency. At the extreme, male and female plants of some mosses appear to be separated by hundreds or even thousands of miles. For example, North American populations of *Tortula pagorum* contain only female plants, European populations appear to be exclusively male, and sporophytes have been observed only in Australia where both males and females occur (Anderson 1943, Stone 1971). In the New York population of *M. mielichhoferiana*, successful sexual reproduction appears to be limited by the infrequent expression of sexuality in spite of the occurrence of both male and female plants.

The percentage of spores that germinate varied greatly among sporophytes both within and between the three populations for which data are available (FIG. 2). On average, sporophytes from the California population had the lowest germination (mean 42.5% ± 11.2 SE) while the two others had almost identical, higher average percentages (New York, 64.9 ± 9.1%; Michigan, 64.8 ± 5.7%). All three populations contained individual sporophytes with very low or zero germination. In fact, about 30% of the sporophytes from the California and Michigan populations contained spore progeny exhibiting lower than 5% germination. Nevertheless, a

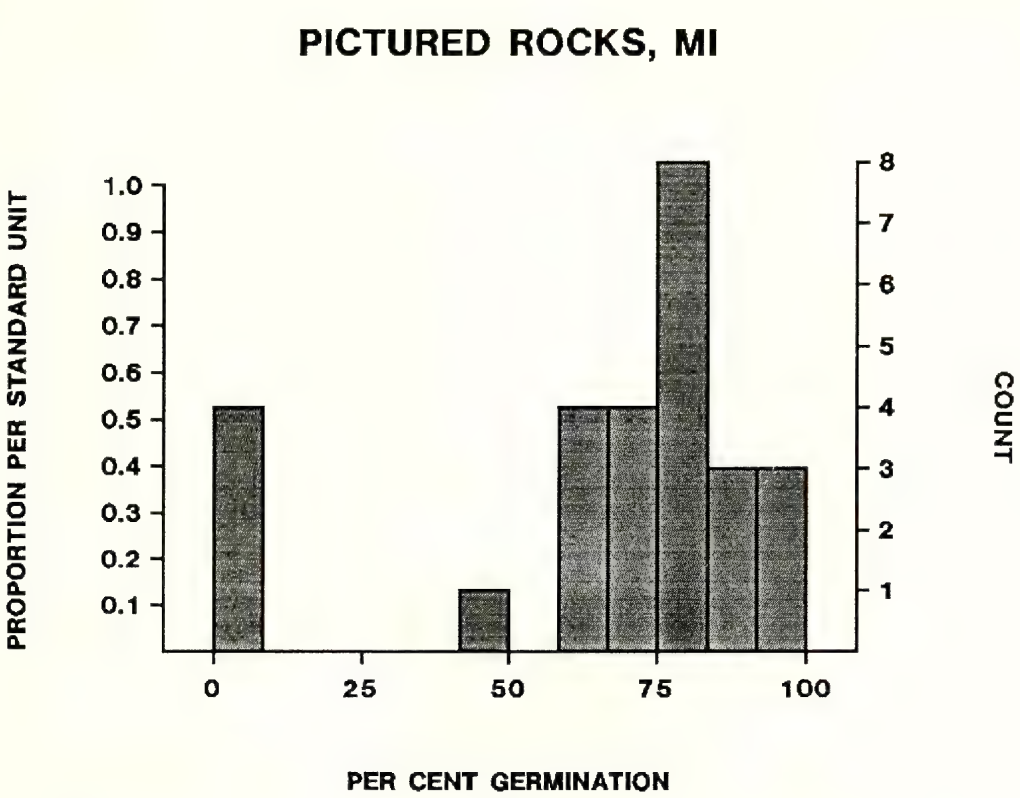


FIG. 2. Germination percentages in families from the Michigan population of *M. mielichhoferiana*. Family means are based on three replicate petri dishes; 35 spores were scored in each dish. The distribution of germination percentages in the California and New York populations were similar, and are not shown. See text for additional discussion.

huge number of viable spores were produced in each of these populations, and numerous studies of other mosses, both rare and common, have shown similar, highly variable germination percentages.

Differences in spore viability between sporophytes may have both genetic and nongenetic determinants. Although "common garden" experiments, including the present study of germination rates, suggest genetic differences, strong environmental effects are also possible, if not likely. In an analogous situation, for example, it has been demonstrated that gametophytic (pollen) vigor can be affected by the nutrient status of the parental sporophyte (Young & Stanton 1990).

Statistically significant differences in sporeling vigor also occurred among families within populations, and among the populations (TABLE 2). On average, plants from the Colorado and Michigan populations grew three times as large as those from California and New York over the same time interval. Tennessee plants were almostly exactly intermediate between these two extremes (TABLE 2). The presence of significant variation in vigor between families of gametophytic plants derived from different sporophytes adds support to the interpretation that family differences have a genetic component. Nevertheless, effects of parental sporophyte nutrition and health on progeny performance is still possible, especially as sporeling growth was measured just 48 hours subsequent to germination. The early growth of sporelings may represent what is essentially an extended germination phase, affected by resources obtained by the spore while still in the sporangium.

TABLE 2. Early sporeling growth in five populations of *Mielichhoferia mielichhoferiana* on Knopp's medium. Mean values (± standard errors) are based on five families (capsules) per population. Spores from each family were inoculated on three replicate petri plates and 10 sporelings were measured on each plate. The analysis of variance for these data is shown below.

POPULATION	SPORELING LENGTH (μm)
California	21.9 ± 1.4
Colorado	60.6 ± 3.5
Michigan	62.9 ± 5.3
New York	20.3 ± 2.3
Tennessee	42.6 ± 8.5

SOURCE	d.f.	SS	MS	F
Populations	3	2416.5	805.5	16.43**
Families (within pops.)	10	1372.1	137.2	2.80*
Error	27	5130.0	190.0	

* = $P \leq 0.01$; ** = $P \leq 0.0001$

TABLE 3. Gametophytic regeneration following 9–14 months of dormancy in Colorado populations of *M. mielichhoferiana*. Each block consisted of 25 gametophytic fragments per population. Integers represent percentages of growing stems out of the 25 for each population.

POPULATION	BLOCK 1	BLOCK 2	BLOCK 3
Eureka Mine	52	44	4
Gothic	55	44	13
Red Mountain Pass South	40	40	8
Red Mountain Pass North	33	40	8
Telluride	16	28	21
Yankee Boy Basin	85	72	25

Differences between the populations were also evident in studies of gametophytic regeneration following nine to fourteen months of dormancy (TABLE 3). When the first block of fragments was initiated the plants had been dried for approximately 9 months, the second block was initiated when the plants had been dried for 12 months, and the last block when the plants has been dried for 14 months. It is clear that plants from all populations lost viability during this period. Indeed, the decline in regeneration was drastic between 12 and 14 months of dormancy. Nevertheless, some consistent population differences were evident. Plants from Yankee Boy Basin, for example, showed the highest percentage regeneration in every experimental block. Conversely, the Telluride population showed the lowest regeneration during both of the first two blocks, improving relative to others in the third block because viability in other populations had declined so greatly. It is noteworthy that the two populations from Red Mountain Pass responded very similarly in every block.

As with the previous experiments, caution should be exercised in assuming that population differences in regeneration result solely from genetic differentiation rather than environmental effects on plants while they were growing in nature. Nevertheless, consistent population differences are definitely suggestive of genetic variance for tolerance of prolonged desiccation and the ability to resume active

growth upon hydration. Similarity between the two Red Mountain Pass populations, in contrast, may reflect underlying genetic similarity. These two populations originated at abandoned copper mines within a few kilometers of each other. The experimental set-up employed in this study is obviously quite unlike conditions in nature, yet variability revealed by this approach may suggest analogous variation in the propensity for asexual dispersal and regeneration under field conditions.

CONCLUSIONS

Understanding the reasons for rarity is fundamental to conservation science and constitutes one of the most fascinating problems in organismic biology. Prerequisite to understanding why some species of plants are rare is the recognition that there are different kinds of rarity (Rabinowitz 1981). The copper mosses constitute a class of plants that have no counterpart among other organisms. They have the odd combination of being extremely widespread but with highly disjunctive and sporadic occurrences.

The copper moss designation for these species is a misnomer not only because some of the species are liverworts and not mosses, but also because their association with copper is inconsistent and sometimes contradictory. A dependence on elevated copper concentrations in the soil is insufficient to explain the rarity of these species. This study assesses the ability of one of the copper mosses, *Mielichhoferia mielichhoferiana,* to reproduce and therefore maintain viable populations, by determining the factors that limit sexual reproduction and by evaluating the viability and vigor of spores and sporelings. In the New York population of *M. mielichhoferiana,* sporophyte formation appears to be limited by the formation of gametangia. However, those spores that are produced are largely viable, and produce relatively vigorous offspring that are capable of sustained gametophytic growth. Although gametophytic growth was measured in this study just days subsequent to germination, these plants have now formed extensive protonema and gametophores in our laboratory.

Population comparisons show that viable spores are the rule and not the exception, and that a significant amount of phenotypic variability occurs within the species. This variability is manifest as both gametophytic growth and the ability to regenerate after prolonged dormancy, and almost certainly reflects some degree of underlying genetic variability. These observations do not suggest that *M. mielichhoferiana* as a species is genetically depauperate. Nevertheless, small populations of limited size increase the risk that chance events combined with habitat destruction pose a significant risk to the long term survival of this rare species.

ACKNOWLEDGEMENT

Funding for this research was provided by NSF grant no. BSR–9020126.

LITERATURE CITED

Andrews, A. L. 1933. The *Mielichhoferia* of northern North America. Bryologist 35: 38–41.

Anderson, L. E. 1943. The distribution of *Tortula pagorum* (Milde) De Not. in North America. Bryologist 46: 47–66.

Antonovics, J., A. D. Bradshaw and R. G. Turner. 1971. Heavy metal tolerance in plants. Adv. Ecol. Res. 7: 1–85.

Basile, D. V. and M. R. Basile. 1988. Procedures used for the axenic culture and experimental treatment of bryophytes. Pp. 1–16 *in* Glime, J. M. (ed.), *Methods in bryology*. Proc. Bryol. Meth. Workshop, Mainz.

Crundwell, A. C. 1976. *Ditrichum plumbicola*, a new species from lead-mine waste. J. Bryol. 9: 167–169.

Hartman, E. L. 1969. The ecology of the "copper moss" *Mielichhoferia mielichhoferi* in Colorado. Bryologist 72: 56–69.

Huenneke, L. F. 1991. Ecological implications of genetic variation in plant populations. Pp. 31–44 *in* Falk, D. A. and K. E. Holzinger (eds.), *Genetics and conservation of rare plants*. Oxford Univ. Press, New York & Oxford.

Kruckeberg, A. R. 1984. *California serpentines*. Univ. Calif. Press, Berkeley.

Longton, R. E. and R. M. Schuster. 1983. Reproductive ecology. *In* Schuster, R. M. (ed.), *New manual of bryology* 1: 386–462. Hattori Botanical Laboratory, Nichinan.

Macnair, M. R. 1989. A new species of *Mimulus* endemic to copper mines in California. Bot. J. Linn. Soc. 100: 1–14.

Persson, H. 1956. Studies in "copper mosses". J. Hattori Bot. Lab. 17: 1–18.

Rabinowitz, D. 1981. Seven forms of rarity. Pp. 205–218 *in* H. Synge (ed.), *The biological aspects of rare plant conservation*. Wiley, New York.

Schatz, A. 1955. Speculations on the ecology and photosynthesis of the "copper mosses." Bryologist 58: 113–120.

Schofield, W. B. 1959. *Mielichhoferia mielichhoferiana* in the Southern Appalachians. Bryologist 62: 248–250.

Shacklette, H. T. 1967. Copper mosses as indicators of metal concentration. Geol. Surv. Bull. 1198G: 1–18.

Shaw, A. J. 1990. Metal tolerance in bryophytes. Pp. 133–152 *in* Shaw, A. J. (ed.), *Heavy metal tolerance in plants: evolutionary aspects*. CRC Press, Boca Raton.

Stone, I. G. 1971. The sporophyte of *Tortula pagorum* (Milde) De Not. Trans. Brit. Bryol. Soc. 6: 270–277.

Young, H. J. and M. L. Stanton. 1990. Influence of environmental quality on pollen competitive ability in wild radish. Science 248: 1631–1633.

Contr. Univ. Mich. Herb. 18:141–147. 1992.

BEEVERIA (HOOKERIACEAE), A NEW GENUS FROM NEW ZEALAND

Allan J. Fife
Botany Institute
DSIR Land Resources
Private Bag
Christchurch, New Zealand

INTRODUCTION

In the course of revising the New Zealand representatives of the Hookeriaceae *sensu* Brotherus for a moss flora of that country, it was concluded that the New Zealand endemic species currently known as *Pterygophyllum distichophylloides* Broth. & Dix. *in* Dix. constitutes an undescribed genus. Given the long-term nature of the New Zealand moss flora project and the recent high level of interest in the Hookeriales (*vide* Buck 1987; Tan and Robinson 1990; Crosby 1974; Allen and Crosby 1986), it is opportune to discuss this species here and to describe a new genus to accommodate it. A monotypic genus, named *Beeveria*, is described with notes on its relationships, synonymy, geographic distribution, and ecology.

BEEVERIA, GEN. NOV.

Pterygophyllum distichophylloides was described by Brotherus and Dixon (Dixon 1915) on the basis of a collection by Donald Petrie from near Auckland. The species has received little subsequent taxonomic attention, probably due to its relative rarity. Treatments by Brotherus (1925) and Dixon (1927) have added little new information. Sainsbury (1955, p. 402) differentiated it from its congeners (in *Pterygophyllum*) by a combination of coloration, and leaf cell and margin characterictics. He also (p. 406) discussed the leaf areolation and the gemmae-bearing pseudopodia and used them as adjunct species characteristics. Sainsbury was the first, and seemingly the only, collector to find this species with capsules. He described the peristome in considerable detail, albeit with some internal inconsistencies (e.g., with respect to exostomial lamellae). While Sainsbury was impressed with the aggregation of peculiar features in *P. distichophylloides*, there is no suggestion that he considered it misplaced within *Pterygophyllum*.

Vitt and Crosby (1972) proposed *Achrophyllum*, a new generic name to replace the illegitimate *Pterygophyllum* Brid., and made appropriate combinations for two New Zealand species. They also stated the unelaborated opinion that *P. distichophylloides* should not be transferred to *Achrophyllum*. Neither Vitt nor Crosby has returned to the problem of the status of *P. distichophylloides*.

Numerous gametophytic and sporophytic features, including the presence of non-homologous vegetative reproductive structures, preclude the transfer of *Pterygophyllum distichophylloides* to *Achrophyllum* Vitt & Crosby (Table 1). There is no genus in the Hookeriaceae *sensu* Brotherus with the combination of gametophytic and sporophytic characteristics found in *P. distichophylloides* and thus a new genus is proposed.

Beeveria Fife, gen. nov.

Plantae vivae citrino-virides, siccae eiusdem coloris vel atrovirides. Caules prostrati, saepe in pseudopodia nuda, 2–3 mm longa, gemmarum capitulo terminata desinentes. Folia haud vel leniter asymmetrica, illa in seriebus dorsalibus ventralibusque ab illis in lateralibus vix divergentia, sicca valde crispata, elliptica, acuta vel apice infirme cuspidata, integra vel crenulata, limbo nullo. Costa singularis, simplex. Cellulae superiores laminales laeves, hexagono-isodiametricae, infirme vel modice collenchymatosae; cellulae marginales diversitatem nullam praebentes. Gemmae in capitulis terminalibus dispositae, anguste fusiformes, 160–240 μm longae, septis transversis 5–9 provisae. Dioeciae. Setae erectae, laeves. Capsulae 1.0–1.5 mm longae. Exostomatis dentes leniter sulcati, ca. 400 μm longi; endostoma membrana basali humili segmentisque perforatis praeditum. Sporae 10–15 μm, virides, subtiliter papillosae.

Beeveria distichophylloides (Broth. & Dix. *in* Dix.) Fife, comb. nov. FIG. 1

Pterygophyllum distichophylloides Broth. & Dix. *in* Dix., Bull. Torrey Bot. Club 42: 106, pl. 9, fig. 11. 1915. TYPE. NEW ZEALAND: near Auckland, 1892, *D. Petrie 800* (BM-Dixon!, WELT!).

Pterygophyllum colensoi Broth. *ex* Dix., Trans. New Zealand Inst. 3(5): 290. 1927, *nom. nud.* BASED ON: Sine loc., *Colenso 3115* (BM *ex* K).

The generic name honors Jessica E. Beever, whose collections and taxonomic work have greatly increased our knowledge of the New Zealand moss flora, especially that of the northern parts of the North Island, where *Beeveria distichophylloides* is most frequently collected.

Plants medium-sized, oily yellow-green when fresh, unchanged or dark-green when dry. Stems prostrate, sparsely to moderately branched, pale brown to yellow, to 4.5 cm, ca. 3 mm wide (including leaves), often ending in naked pseudopodia 2–3 mm long and terminated by a capitulum of gemmae; in cross-section with a distinct central strand, lacking a hyalodermis, with 2–4 cortical cell layers with moderately thickened walls; rhizoids on lower portion of stem dense, pale brown, ± smooth, much-branched; pseudoparaphyllia foliose, lanceolate, ca. 300–400 μm long. Leaves inserted in 6 ranks, imbricate, complanate, nearly symmetric, those in dorsal and ventral ranks scarcely differentiated from those in lateral ranks, strongly crisped when dry, elliptic, tapered to acute or weakly cuspidate apices, plane, not concave, unbordered, entire (often somewhat crenulate due to collapsed walls of marginal cells in dry material), (1.0–)1.3–2.5(–2.8) × 0.5–1.3 mm; costa single, ill-defined, ca. 35–60 μm wide at midleaf, markedly dilated in lowest third or more, unbranched, ½ to more than ¾ the length of the leaf, in cross-section biconvex, lacking stereids; upper laminal cells smooth, thin-walled (ca. 2 μm at thinnest point), weakly to moderately thickened at corners, hexagonal-isodiametric, 24–42 μm diam., gradually becoming ± oblong and non-collenchymatous toward base; marginal cells and alar cells not differentiated. Gemmae borne in terminal capitula, narrowly fusiform, 160–240 μm long, with 5–9 transverse septa. Dioicous; perigonia not seen (nor did Sainsbury, 1955, p. 406). Perichaetial leaves ovate-lanceolate, ecostate, ca. 1.2 mm long. Setae lateral, ca. (7–)9–11 mm long, erect, smooth, twisting weakly to the left throughout, red, ca. 150 μm diam., in cross-section lacking a hyalodermis, with 1–2 layers of thick-walled cortical cells and an ill-defined central strand; capsules pendent, ovoid from a short neck, 1.0–1.5 mm

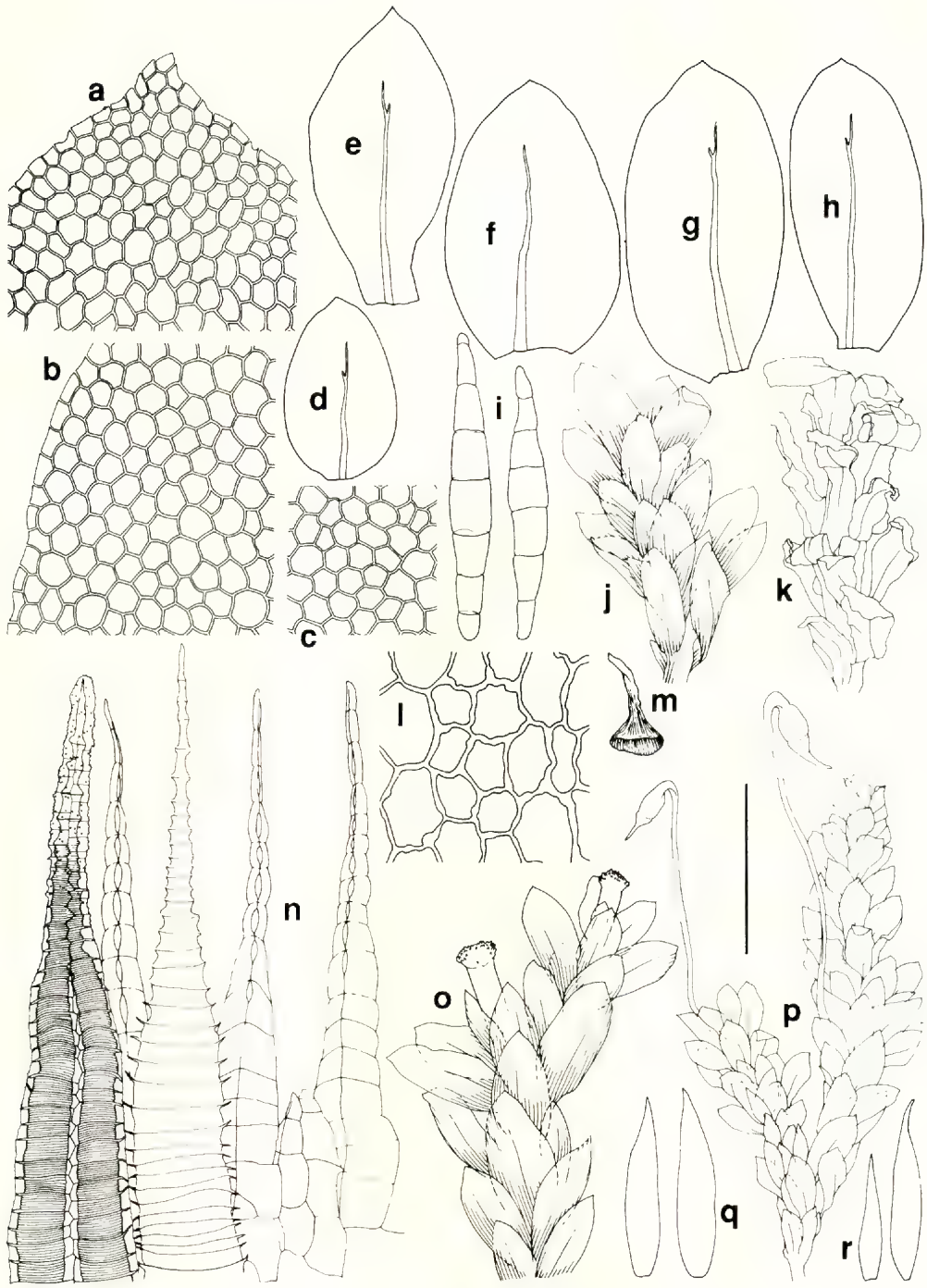


FIG. 1. *Beeveria distichophylloides*. a. Leaf apex. b. Margin at midleaf. c. Upper laminal cells. d–h. Leaf outlines. i. Gemmae. j. Moist stem. k. Dry stem. l. Exothecial cells. m. Operculum. n. Portion of peristome, showing outer and innter surfaces of exostome tooth, endostomial membrane and segments. o. Moist stem with pseudopodia. p. Moist stem with sporophytes. q, r. Perichaetial leaves. Scale = 165 μm for a–c, 1000 μm for d–h, q, r; 2300 μm for j, k, o; 100 μm for i, l, n; 3500 μm for p; 1400 μm for m. From *Fife 6068* and *Sainsbury 4388* (both CHR).

FIG. 2. Total distribution for *Beeveria distichophylloides*. Distribution dots centered on NZMS 260 1:50,000 topographic map sheets.

long, weakly constricted below the mouth and smooth when dry, reddish-brown; exothecial cells oblong to isodiametric, firm-walled, rather weakly thickened at corners, 12–18 μm in greatest diam.; annulus well developed, falling with the operculum; operculum long-rostrate from a conic base, ca. 0.8 mm long; exostome teeth yellow, lanceolate with a rather distinct shoulder, bordered, weakly furrowed (gap between portions of tooth less than 6 μm, extending to less than ⅔ the length of the tooth, not visible with stereoscope), ca. 400 μm long, finely cross-striate below, baculate above, with adaxial lamellae projecting as weak trabeculae (6–9 μm long near base of tooth); endostome pale yellow, with basal membrane 100–120 μm high, segments ca. 260 μm long, nearly equaling the teeth, keeled and weakly perforate, papillose, cilia absent. Spores (10–)12–15 μm, green, very finely papillose. Calyptra mitrate, smooth, lobed at base [description from Sainsbury (1955, p. 405)].

Distribution. Beeveria distichophylloides is known only from New Zealand. There, it has a scattered distribution between latitudes 35° and ca. 42°19′S on the two main islands. It is recorded from North Auckland, Gisborne, Hawke's Bay, Nelson, and Westland land districts (Fig. 2). It is not known from any offshore island except D'Urville Island (Nelson Land District). It displays a distribution similar to that of nikau palm (*Rhopalostylis sapida*) and several mosses of northern affinities, e.g., *Braithwaitea sulcata, Catharomnion ciliatum, Ctenidium pubescens,* and *Tayloria callophylla.*

Ecology. Beeveria distichophylloides occurs on moist, shaded rock (usually, if not always, limestone) and clay or marl soil, often in association with stream margins or beds of intermittent watercourses. *Distichophyllum microcarpum* and *Achrophyllum dentatum* are frequent associates. It ranges in altitude from ca. 90–

TABLE 1. Comparison of character states in *Beeveria* and *Achrophyllum*.

Character	State in *Beeveria*	State in *Achrophyllum*
Dry coloration	Yellowish green	Brown or black
Shape of gemmae	Fusiform, transversely septate	L- or T-shaped, transversely septate
Location of gemmae	Terminal on pseudopodia	Epiphyllous on intramarginal cells
Nature of exostome tooth furrow	Less than 6 μm wide; not visible with stereoscope (40–50×)	Greater than 30 μm wide; visible with stereoscope
Length of exostome trabeculae	6–9 μm	18–24 μm
Height of endostomial basal membrane	ca. 100–200 μm	ca. 300 μm

300 m on the North Island and from 20–600 m in the northwest portion of the South Island.

Discussion. The generic name *Pterygophyllum* Brid. (Mant. Musc. 149. 1819) is illegitimate; a proposal to conserve this name against *Achrophyllum* Vitt & Crosby (Margadant *et al.* 1972) was rejected. A combination in *Achrophyllum* for *P. distichophylloides* has never been published. TABLE 1 summarizes the gametophytic and sporophytic features which distinguish *Beeveria* and *Achrophyllum*.

In *Beeveria,* gemmae occur in terminal capitula atop short pseudopodia and are fusiform and transversely septate. The pseudopodia of *Beeveria* are reminiscent of the unrelated genus *Aulacomnium*.

Sporophytically, the features that separate *Beeveria* from *Achrophyllum* are quantitative rather than qualitative (TABLE 1), but in aggregate they support generic segregation. In *Beeveria,* exostome teeth are weakly furrowed, short, and weakly trabeculate. The furrow is less than 6 μm wide at base, extends ca. ⅔ the tooth length, and is not visible under stereoscope; the teeth are ca. 400 μm high, with lower trabeculae 6–9 μm long. In *Achrophyllum quadrifarium* (the generitype) the teeth are strongly furrowed, longer, and strongly trabeculate. The furrow is 30–36 μm wide at base, extends ¾ the length of the tooth, and is clearly visible under the stereoscope; the teeth are more than 700 μm high, with lower trabeculae 18–24 μm long. In *Beeveria,* endostomial segments are perforate and arise from a basal membrane ca. 100–120 μm high, while in the generitype of *Achrophyllum* segments are non-perforate and arise from a basal membrane ca. 300 μm high.

Buck (1987) synthesized the large amount of recent information and opinion (*vide* Tan and Robinson 1990; Crosby 1974; Allen and Crosby 1986) concerning the classification of the Hookeriales and proposed a reorganization of the order into five families. Buck's familial concepts place considerable emphasis upon gametophytic features and, despite some criticisms which have been leveled at them (*cf.* Tan and Robinson 1990), they are accepted here. Buck reduced the Hookeriaceae to only six genera (*Achrophyllum* Vitt & Crosby, *Cyathophorella* (Broth.) Fleisch., *Cyathophorum* P.-Beauv., *Dendrocyathophorum* Dix., *Hookeria* J. E. Sm., and *Schimpero-*

bryum Marg.); all other genera in Brotherus' Hookeriaceae are placed in four segregate families. He placed *Hookeria, Achrophyllum* and *Schimperobryum* in one "lineage" within his restricted Hookeriaceae. If Buck's evolutionary hypothesis is accepted, the lack of a central strand, the large, unbordered leaves, the short, hexagonal and porose leaf cells, the presence of pseudoparaphyllia, and other features in *Beeveria* dictate its inclusion in both the restricted family and in the lineage "centered around *Hookeria*." Within the "lineage" the nature of the leaf cells and the single, forked costae (interpreted here as synapomorphies) of *Achrophyllum* and *Beeveria* differentiate them collectively from *Hookeria* and *Schimperobryum*. By this interpretation, *Beeveria* and *Achrophyllum* are sister taxa, forming a clade whose relationship to *Hookeria* and *Schimperobryum* is not resolved.

The presence of pseudopodia and the fusiform, apical gemmae of *Beeveria* and the L- or T-shaped, intramarginal gemmae of *Achrophyllum* are apomorphies which differentiated the two allied genera. They suggest that *Beeveria* was not the ancestor of *Achrophyllum*, and the acceptance of *Beeveria* does not render *Achrophyllum* paraphyletic.

Differences in coloration of dried plants provide further distinction between *Beeveria* and *Achrophyllum*. The relatively weakly collenchymatous thickenings of the leaf cells, remarked upon by Sainsbury (1955, pp. 402, 406), are not considered significant as this feature varies markedly among various species of *Achrophyllum*.

Sainsbury's statements (1955, p. 406) that the exostome teeth of *Beeveria* (*sub Pterygophyllum*) *distichophylloides* lack both (adaxial) lamellae and median furrows, and that the median divisural line is more conspicuous relative to other species which he included in *Pterygophyllum*, are incorrect. Both adaxial (ventral) lamellae and a median furrow are present (but the latter is not visible under a stereoscope) and the "zig-zag" divisural line is no more conspicuous than in *Achrophyllum quadrifarium*.

No other genus in the Hookeriales bears gemmae in the manner of *Beeveria*. The one genus in the order with structures vaguely similar, the monotypic American-African genus *Adelothecium* (placed in a monotypic family by Buck [1987]), bears gemmae on axillary stalks on specialized microphyllous branches. The thick-walled, porose leaf cells, brownish pigmentation, lack of a central strand, and ascendent habit of *Adelothecium* are among many features which preclude the placement of *B. districhophylloides* in, or even close to, that genus.

ACKNOWLEDGMENTS

Illustrations were prepared by Sabrina Malcolm. Janie Glasson and Mary-Ann O'Brien provided help with preparation of the distribution map and Elizabeth Edgar translated my description into Latin. Phil Garnock-Jones and Bryony Macmillan provided criticism that allowed improvement of the manuscript.

Howard Crum has provided guidance for many years and it is a pleasure to dedicate this contributions to him on the occasion of his 70th birthday.

LITERATURE CITED

Allen, B. H. and M. R. Crosby. 1986. A revision of the genera *Pilotrichidium* and *Diploneuron* (Musci: Hookeriaceae). J. Hattori Bot. Lab. 61: 45–64.

Brotherus, V. F. 1924–1925. Musci. *In:* A. Engler and K. Prantl (eds.), *Die natürlichen Pflanzenfamilien, ed. 2,* Bande 10–11. Engelmann, Leipzig.

Buck, W. R. 1987. Taxonomic and nomenclatural rearrangement in the Hookeriales with notes on West Indian taxa. Brittonia 39: 210–224.

Crosby, M. R. 1974. Toward a revised classification of the Hookeriaceae (Musci). J. Hattori Bot. Lab. 38: 129–141.

Dixon, H. N. 1915. New and rare Australasian mosses, mostly from Mitten's herbarium. Bull. Torrey Bot. Club 42: 93–110.

———. 1927. Studies in the bryology of New Zealand, with special reference to the herbarium of Robert Brown. Part 5. Bull. New Zealand Inst. 3: 239–298.

Margadant, W. D., H. A. Miller and C. M. Matteri. 1972. Proposal for the conservation of the generic name *Pterygophyllum* Brid. 1819 in Musci. Taxon 21: 536.

Sainsbury, G. O. K. 1955. A handbook of the New Zealand mosses. Bull. Roy. Soc. New Zealand 5: 1–490.

Tan, B. and H. Robinson. 1990. A review of Philippine hookeriaceous taxa (Musci). Smithsonian Contr. Bot. 75: i–iv, 1–31.

Vitt, D. H. and M. R. Crosby. 1972. *Achrophyllum*—a new name for a genus of mosses. Bryologist 75: 174, 175.